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A. G. TANSLEY

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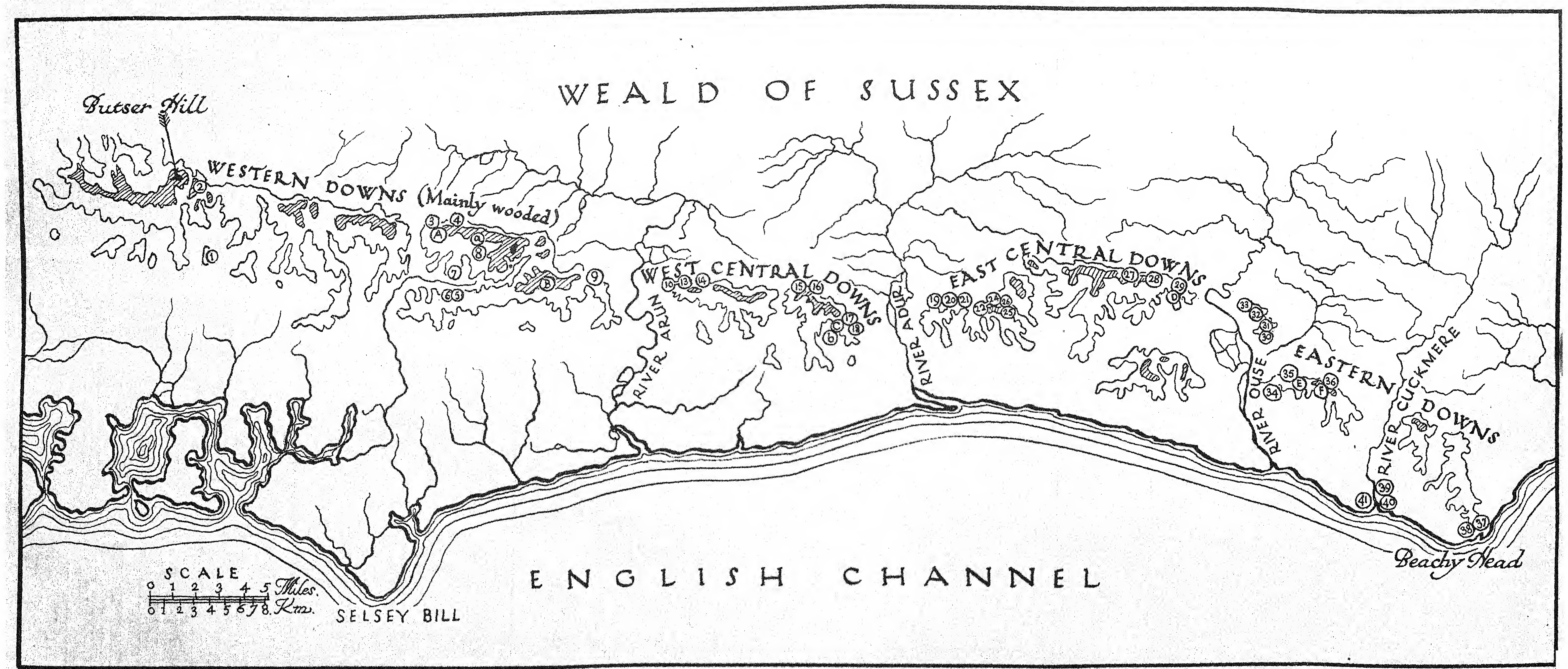
ERRATUM

Vol. XIV, p. 165, par. 4, line 1, par. 5, line 1, and p. 166, seventh line from bottom of page. *For* "phosphates" *read* "phosphatids."



Sketch-map of the South Downs from Butser Hill to Beachy Head, kindly drawn by Mr H. Tomlinson of the Cambridge University School of Architecture. The lowest contour line drawn is that of 400 feet; 600–800 feet diagonally hatched; above 800 feet, black. The numbers (1–41) mark the approximate locations of the areas of chalk grassland described in the paper; A–F mark the "chalk heaths" described; *a* and *b* the heaths.

VOLUME XIV FEBRUARY, 1926 No. 1

STUDIES OF THE VEGETATION OF THE ENGLISH CHALK

IV. A PRELIMINARY SURVEY OF THE CHALK GRASSLANDS OF THE SUSSEX DOWNS

BY A. G. TANSLEY AND R. S. ADAMSON.

(*With Plate I and a Sketch-map.*)

CONTENTS.

1. INTRODUCTION. DESCRIPTION OF THE REGION

The data presented in this paper were mostly collected by the authors in August, 1921, during the course of a traverse of the South Downs from War Down, just east of Butser Hill in Hampshire, to Beachy Head in Sussex, where the chalk range is cut off by the sea—a total distance, in a straight line, of 56 miles, or about 90 km. The actual course of the chalk range is somewhat longer, about 62 miles or 100 km., since it is by no means straight throughout its length. Not every mile of this distance was traversed—the most considerable gaps left being between War Down and Cocking (a distance of 10 miles), between the Devil's Dyke and Ditchling Beacon (6 miles) and between Alfriston and Beachy Head (8 miles). The line of the north escarpment of the Lower Chalk facing the Weald was mostly followed, and about 20 of the 49 areas examined were situated on the escarpment itself—the main object of the survey being to obtain data from plant communities situated on soils immediately overlying and obviously derived directly from the chalk itself over a fairly extensive stretch of country, and these are most commonly

encountered on moderate or steep slopes. A certain number of areas lying off the escarpment are, however, included in the tables, some on slopes with genuine chalk soil, others taken from "chalk heath" (6 areas) and "heath" (2 areas) developed on the chalk plateau. Data from the communities of these last two categories are given in a separate table (Table II pp. 22, 23).

The region was revisited in June, 1923, by one of the authors in company with Mr H. Gilbert-Carter, with the object of supplementing the original lists by including species not observable at the end of the severe drought of 1921. Many of the areas were re-listed and a few fresh ones listed, but little that was new was discovered, the principal species observed in 1923 and not seen in 1921 being *Senecio campestris* (*Cineraria integrifolia*), a species whose sub-aerial shoots had no doubt dried up and disappeared during the very hot summer of the earlier year. Many more records of orchids were expected in 1923, but very few were obtained.

The lists of Bryophytes are no doubt incomplete, partly owing to the season and weather of the year when they were compiled, though all the species which form important constituents of the Sussex chalk grassland are certainly included. Very little attention was given to the Bryophytes on the second series of visits. It is noteworthy that no Pteridophyte was met with on any of the 49 areas examined, with the exception of *Dryopteris filix-mas*, which had established itself along with other woodland plants on one of the heath areas (*a*) almost surrounded by forest. Woody plants invading the grassland have been omitted (with the exception of *Calluna*, *Erica cinerea*, *Ulex nanus* (*minor*) on the "chalk heaths" and "heaths") but have been alluded to in the short descriptions on pp. 5–14.

The approximate locations of the areas listed are shown in the Sketch-map (1–41, A–F, a, b). The sizes of the areas listed are not constant. The attempt was made to get as complete a list as possible from each place, so far as the vegetation appeared uniform and the habitat (including aspect) appeared constant. Probably the size of the area included in each list varied from about a quarter of an acre to about an acre (say an eighth to half a hectare).

The first two areas, situated in Hampshire, are selected from the lists made during the more detailed investigation by the authors of "The Chalk Grasslands of the Hampshire-Sussex border" which forms the third of these "Studies" (This Journal, **13**, pp. 177–223). They are as typical examples as could be chosen of the extreme western chalk grasslands of the region under consideration. These two lists are the longest of any, partly because the areas are relatively large and were visited several times in different years and at different seasons. They lie just to the west of the well-wooded western region of the Downs and are not far distant from extensive woods. Passing eastward from these there is a considerable gap in the series, extending to Cocking, but the next seven areas (3–9) are all situated on the well-wooded Western Downs, where not only much of the escarpment but great areas of

plateau, dipslope and valley side are covered with forest; and the lists show that there is no great difference between the grassland areas in this region and the two distant Hampshire ones. On the next stretch (10–18), which we have called the West-central Downs, escarpment woods are almost lacking along the western section from Amberley to the Washington gap, but are practically continuous along the eastern section, from Washington to Steyning. Here the plateau and dipslopes are almost destitute of wood but are much covered with heath and scrub, alternating with arable land. At this point too, *Bromus erectus*, very local indeed in the west, becomes locally dominant over considerable areas, and *Brachypodium pinnatum* was met with for the first time. *Filipendula hexapetala* also, so abundant on many of the Eastern Downs, had not been encountered west of this region. *Senecio campestris*, again, was not met with west of the East-central Downs, and *Phyteuma orbiculare* is much commoner in the centre and east. *Campanula glomerata*, on the other hand, was not seen east of the West-central Downs. All six of these species are characteristic of chalk grassland, so that there seems to be a real floristic transition in the region of the Central Downs, running parallel with the diminution and disappearance of chalk woodland. This does not mean, of course, that these species do not occur on the chalk of both East and West Sussex. They are all six recorded in Watson's *Topographical Botany* and *Supplement* from both, though they were not seen by us on our traverse; and the differences in their abundance and frequency on the Eastern and Western Downs must be very great.

The East-central line of Downs may be divided into three parts: a western straight portion from Beeding to the Devil's Dyke (19–26), entirely destitute of woods, a central northward curve (not examined but with a few plantations) extending to just beyond the London-Brighton road, and an eastern straight portion (27–29) from Ditchling Beacon to Mount Harry (Lewes), again with very little wood. Then we come to the isolated Mount Caburn group of Downs (30–33) just east of Lewes, and finally to the Eastern Downs beyond the Ouse valley, curving south-east and south from the Firle Beacon region to Beachy Head (34–38). The last three areas (39–41) were taken on each side of the Cuckmere valley, and, with 37 and 38, were quite close to the sea. On the escarpments of none of these Eastern Downs is there more than an occasional plantation or patch of scrub, though the plateau and dipslope are in places much covered by scrub or heath.

Apart from the wide divergence between the two ends of the South Downs in the amount of woodland they bear, there are other features of difference. The western end is at present much more generally and heavily infested with rabbits, apparently because the Western Downs are a region of great estates, largely maintained for the sporting interests of their owners, while the Central and Eastern Downs are a region of farms in which rabbits are not encouraged. This difference apparently affects the dominant grasses, *Avena pratensis* and

A. pubescens, as well as *Bromus erectus*, being much more prominent in the centre and east than in the west. *Anthoxanthum odoratum*, too, is generally a more abundant constituent of the chalk grassland east of the River Arun.

A leading physiognomic difference is the frequent occurrence in the region of the Central and Eastern Downs of tall close herbage on the steep northern slope of the main escarpment. This never exists where rabbits are abundant. It is dominated by a variety of grasses, not only the Avenae and *Bromus erectus*, but also locally by *Arrhenatherum elatius*, *Deschampsia caespitosa*, *Poa pratensis*, *Festuca rubra*, and in extreme cases by *Festuca elatior*, towards the damper bottom of the slope. (See areas 10, 11, 14, 19–24, 27, 28, 35, 36.) *Primula veris*, *Scabiosa succisa*, and *Rumex acetosa* are rather characteristic species of these slopes, while *Festuca ovina* and many of the small herbs of closely pastured chalk grassland are considerably diminished in abundance. The soil is generally fairly deep and often rich in humus, but it retains a distinctly high alkalinity (*p*H, 7·2—7·8) in the surface 2 or 3 inches. This meadow-community is distinct, as regards dominants and soil, from the well known chalk grassland dominated by *Festuca ovina*. But we see no reason to separate it from the latter at all sharply, since most of the associated list of species is the same. It is simply a result of the increase in the moist shaded conditions of the steep northern slope of the tall grasses, in the absence of continuous grazing. This leads to increased competition and a tendency to elimination of the smaller plants. The soil is characteristic (see p. 15).

Mosses are on the whole much less abundant in the grassland of the Central and Eastern than in that of the Western Downs, but some of the steep northern slopes just described carry a considerable moss flora. Nowhere, however, east of the Arun was the dominance of mosses on northern exposures of the Hampshire Downs at all paralleled, except on one northern exposure (23) of exceptionally steep slope, probably artificial and suggesting (by the presence also of *Tussilago farfara*) an early phase of development. This phenomenon is doubtless correlated with the rainfall and humidity. The Western Downs nearly to the Arun and a small area round Ditchling Beacon receive between 31 and 34 inches, while most of the Central and Eastern Downs receive between 28 and 31. The southern exposures examined are, as might be expected, notably poor in bryophytes, and some are quite destitute of them. This is specially marked in the extreme eastern region near the sea, which is also poor in flowering plants, the few submaritime species not compensating for the poor development of the general list. Areas 39, 40 and 41 are situated in a region which receives less than 25 inches of rain[1].

Besides the species mentioned on p. 3 certain others show a preponderating

[1] The rainfall data are taken from **Hall** and **Russell's** *Agriculture and Soils of Kent, Surrey, and Sussex* (1911) and represent a 10-year average. The particular 10-year period available was a dry one, and the figures are probably rather more than an inch below the averages that would result from a longer period.

distribution in east or west, according to our records. Though some of these may be devoid of distributional significance we add the more striking for what they may be worth.

Species more frequent in the east.

Anthyllis vulneraria, especially abundant around Lewes, though locally abundant here and there in the centre and west.

Arabis hirsuta, only seen in the east-centre and east.

Hippocrepis comosa, very local in the west, is met with much more frequently in the centre and east, and though always local, is quite often dominant in small areas, colouring certain downsides bright yellow in June.

Poterium sanguisorba, though one of the most constant and abundant constituents of chalk and limestone grassland in England as a whole, is not so constant in West Sussex and Hampshire as in East Sussex.

Species more frequent in the west.

Gentiana amarella on 12 (more than half) of the areas (nearly always marked as "occasional") west of the Devil's Dyke, was only seen on one area east of this point.

Helianthemum vulgare on five areas in the western, and only one in the eastern half.

Leontodon autumnalis on 11 areas in the western and only one in the eastern half.

Origanum vulgare on five in the western, one in the eastern half.

2. DESCRIPTIONS OF AREAS EXAMINED

A. WESTERN DOWNS (mostly wooded).
(London-Portsmouth Road to River Arun.)

1. *Chalton Down* (Hants). Slope 24–32° E., alt. 350 feet, side of a valley on the Upper Chalk, three miles S. of the escarpment of the Lower Chalk. Herbage 2–3 in., pastured by sheep but not too heavily. Dotted with juniper bushes, and clumps of scrub in places. Soil 4 inches to the layer of large chalk lumps and another 4 inches to fissured upper surface of chalk *in situ*.

2. *War Down* (Hants). Slope 16° E., alt. 600–700 feet. Close to escarpment of Lower Chalk. Herbage 3–4 in. pastured. A good list of mosses. Eight inches of brown to grey-brown humous loam mixed with small chalk fragments to surface of fissured chalk.

3. *Cocking*. Slope 18–20° W.N.W., alt. 500 ft., with beechwood and calcicolous coppice on one side. Herbage 1 in., rabbit eaten. *Carex flacca* leading, almost dominant, much less *Festuca ovina* than usual. *Hippocrepis comosa* locally dominant. Soil 2 in. of humous loam matted with roots: then 3 in. with chalk lumps, some 4 in. diam. Partly disintegrated chalk *in situ* at 5 in.

4. *Heyshott* (escarpment due S. of). Slope 32° N., alt. 700 ft., chalk scrub with much ash to E. and W. Herbage 2–3 in. mostly dominated by mosses,

but no great variety. Severely rabbit-eaten but somewhat protected by mosses. Frequent pure clumps of *Dicranum scoparium* 6 in. across, with leaves of *Carex flacca* (the most abundant species after the mosses) striking through; *Cirsium acaule* next in abundance. Soil 2 in. of surface, then at least 8 in. with loose chalk lumps. Seedlings of *Fraxinus*, *Cornus* and *Crataegus* nibbled over by rabbits.

5. *East Dean* (roadside, sometimes lightly pastured). Slope 10° W., alt. 400 ft. Herbage 4–8 in. (1921) 3–12 in. (1923) forming tussocks, grasses dominant. Very occasional young plants of *Corylus*. Soil a brown loam, 0–5 in. firmly held by roots, 5–10 in. with lumps of weathered chalk. Upper fissured surface of chalk *in situ* at 10 in.

6. *East Dean* (opposite 5, pastured field), slope 10–12° E., alt. 400 ft. Herbage 2–4–6 in. Turf thick. Soil a brown loam 0–5 in. held by roots as in (5), chalk *in situ* at 7 in.

7. *East Dean* (cattle-pastured grassland), slope 18° S., alt. 300 ft. Herbage 2–3 in. Mainly a chalk flora, but *Sieglingia decumbens* and *Potentilla erecta* local. Soil round roots of former gave no effervescence with dilute HCl: in other places on surface a moderate to strong effervescence.

8. *East Dean*. Enclave of grassland enclosed in North Side and Tegleaze beechwoods, alt. 500 ft. Heavily rabbit-eaten. Soil very chalky to surface. *Poterium sanguisorba* absent. Poor flora.

9. *West Burton Hill*. Slope steep to N., alt. 400 ft. Fairly typical chalk pasture with *Festuca ovina* dominant. Soil blackish brown, chalk lumps at 3 in. Chalk *in situ* at 6 in.

B. West-central Downs. River Arun to River Adur.

10 and 11. *Amberley Mount*. West and W.N.W. exposures, alt. 400–500 feet. Thick tall grass herbage with tall inflorescences of *Avena* spp., *Arrhenatherum*, *Bromus erectus*, *Dactylis*, *Trisetum*, etc., not recently pastured. A few bushes of *Crataegus* and seedlings.

12. *Amberley Mount*. Slope 18–25° (32°) N., alt. 400–500 feet. Passing eastward to this exposure from the last the tall herbage gradually disappears as a hollow with a rabbit burrow complex is approached (untouched flowering grasses at 150 yards from this complex). Soil light brown, showing gradual transition from surface to chalk *in situ* at 12 in. Many root systems are present at this depth.

13. *Amberley Mount*, further east, slope 22–32° (34°) N., alt. 400–500 feet. Turf somewhat rabbit eaten, 2–4 in. Seedling *Quercus* and *Fraxinus*.

14. *Rackham Hill*. Slope 32–37° N., alt. 500–600 feet. Herbage 9–18 in. Tall grasses dominant, mainly *Avena pratensis*, *Dactylis glomerata* and *Agrostis alba*: inflorescences 24–30 in. Soil grey-brown with chalk lumps at 3 in. and down to 10 in. (chalk *in situ*): roots abundant to 10 in. Isolated bushes of *Juniperus*, *Crataegus*, *Fraxinus*.

15[1]. *Chanctonbury* (west of). Slope 15° N., alt. 500 feet, herbage 1–3 in., moderately rabbit-eaten. Mainly a chalk flora, but *Sieglingia decumbens*, *Agrostis tenuis*, *Potentilla erecta* and *Calluna vulgaris* present. Flints and fragments of chalk at 2 in. and downward to 7 in. where chalk is *in situ*.

16[1]. *Chanctonbury* (due N. of Ring). Lower part of escarpment wooded. Upper part, slope 27° N., alt. 600–700 feet. Turf about 2 in.

Poterium sanguisorba and *Carex flacca* practically co-dominant, the common mosses abundant. Seedlings of *Fraxinus*, *Corylus*, *Acer pseudoplatanus*, *Fagus*. Locally *Rubus leucostachys*. Soil looks chalky to surface, small chalk lumps in second inch. Large flat chalk blocks (probably *in situ*) with soil between from 4 to 8 inches from surface.

17[1]. *Steyning Round Hill*. Slope 27° N., alt. 400–500 feet. *Bromus erectus* dominant generally, with *Brachypodium pinnatum* locally dominant. Herbage deep and thick, 9–12 in. Scattered Junipers with young *Ilex* and *Fraxinus* in their shelter: also *Viburnum lantana*, *Rosa* sp. and *Solanum dulcamara*. Soil with small chalk lumps immediately below turf, chalk *in situ* at 6 in.

18. *Steyning* (above Maudlin Farm). Slope 5° S.E., alt. 400–500 feet. Numerous mixed grasses. Scattered bushes of *Crataegus*, *Juniperus*, *Prunus spinosa*, *Rosa micrantha*, *Rubus rusticanus*. Soil very shallow, chalk showing on surface.

C. East-central Downs. River Adur to River Ouse.

19. *Tottington Hill*. Slope 15–25° N., alt. 300–400 feet. Very good uniform grassland. Grasses decidedly dominant, *Avena pratensis* and *Bromus erectus* preponderating; then *Poterium sanguisorba*. *Primula veris* forming marked "families" and "clans." Herbage 6–8 in. Inflorescences 2–3 feet. Scattered *Crataegus* bushes. *Festuca rubra* (dominant on ant hills). Soil top 3 inches, shrinks strongly to hard black cake on drying; chalk lumps at 3 to 4 inches.

20. *Truleigh Hill*. Slope 30–32° N., alt. 600 feet. Grasses dominant. Herbage 10–12 in. Inflorescences 2 feet. Seedling *Fraxinus*.

21. *Edburton Hill*. Slope 30–35° (in steepest part) N., alt. 500–600 feet. The tall grasses (including *Poa pratensis*) and *Poterium* very abundant: *Festuca ovina*, *Bellis*, *Linum catharticum*, etc., especially in short grazed turf. Chalk lumps in soil at 4 in. Top inch of soil shrinks to blackish brown cake on drying.

22. *Perching Hill*. Slope 32–37° (in steepest part) N., alt. 400–500 feet. Slope with narrow terraces, edges occupied by tall grasses. *Festuca ovina* grazed turf between. (Cf. Cliffe Hill, Lewes, 32.) Herbage 1 (grazed) to 12 inches (tall grasses). Mosses not abundant. Soil 3 in. of surface loam with many small chalk lumps beginning 1 in. from surface. 3–7 in. disintegrated chalk. At 7 in. chalk *in situ* much fissured and broken.

23. *Between Perching and Fulking Hills*, a steep slope 37–40° (extreme 42° at steepest—perhaps cut) N., alt. 450 feet. Chalk grassland, but barely

[1] *See* Table I, p. 20, for rather unexpected *p*H values.

stable in steepest places. *Tussilago farfara* with small leaves, probably a relict of an earlier stage of succession consequent on cutting the chalk. Much moss—*Hylocomium triquetrum* and *H. splendens* locally dominant: also great quantities of *Nechera crispa* on bare patches. Over 40° the soil tends to slip and open, though mosses such as *Hypnum molluscum* and *N. crispa*, in which grow herbs and grasses, may maintain themselves on the sides of cuttings at 45° or even 50°.

24. *Fulking Hill.* Slope 22–24° N.E., alt. 400–500 feet. Herbage 4–12 in. *Avena pratensis* generally dominant, *Festuca rubra* frequent to abundant.

25. *Devil's Dyke.* Slope about 30° N.N.W., alt. 400–500 feet. Herbage 6 in. Moss layer 2 in. thick. *Achillea, Anthoxanthum, Primula veris, Koeleria gracilis, Rumex acetosa, Scabiosa* spp. present (absent in 26). Soil 3 in. to chalk *in situ*.

26. *Devil's Dyke.* Opposite slope, about 30° S.S.E., same altitude. Herbage 1½–4 in. Soil 2–3 in. to chalk *in situ*. Grasses only sparse, no mosses. Species mentioned under (25) absent. *Cirsium acaule, Hippocrepis* markedly more abundant than in (25), *Helianthemum* present. These and similar differences from (25) seem entirely a result of aspect.

27. *Escarpment due S. of Goat Farm, Westmeston* (one mile E. of Ditchling Beacon), in and above angle of V-shaped plantation. Slope 35–37° N., alt. 600–700 feet. On upper part of slope herbage 8 in., tall grasses dominant and tending to smother other plants. On lower part (between arms of V-plantation) herbage 18 in., very tall grasses overwhelmingly dominant (inflorescences 3 feet), rest of flora very poor: *Festuca elatior* generally dominant, *Arrhenatherum elatius* locally dominant: *Pimpinella saxifraga* and *Centaurea nigra* the main species maintaining themselves in the thick tall grass. This locality represents the most extreme dominance of grasses met with on a shallow chalk soil. The shelter of the plantation is evidently an additional factor. The plantation is composed of *Pinus austriaca, Picea excelsa, Quercus ilex, Acer pseudoplatanus, Fraxinus excelsior*, with *Sambucus nigra* colonising it. *Fraxinus* is the only woody plant observed to be colonising the sheltered grassland, in which *Anthriscus silvestris* occurs (rarely). Soil blackish, shrinks and hardens on drying.

28. *Escarpment N. of Plumpton Plain.* Slope 30° N., alt. 500–600 feet. Herbage 12 in. The same grasses dominant as in (27), but *Festuca elatior* not so predominant. *Crataegus* bushes scattered, with *Sambucus*. Soil very loose dark humus going down at least 8 inches, with chalk lumps almost immediately below surface.

29. *Mount Harry.* Slope 30° N., alt. 400–600 feet. (Pl. I, fig. 1.) Herbage tussocky, cattle-pastured, 6–8 in. high. Much moss. *Poterium* abundant to subdominant. Scattered *Crataegus* frequent, *Viburnum lantana* occasional, Sycamore seedlings. Soil 3 to 4 inches of dark humous loam with small chalk articles, then disintegrated chalk with soil between. Solid chalk *in situ* at 10 in.

FIG. 1. Typical pastured chalk grassland on North escarpment (Area 29), alt. 400–600 ft. with *Crataegus* shrubs and local rabbit burrows. Planted beechwood behind. Arable cultivation on Weald plain below. Mount Harry, Lewes (East-Central Downs).

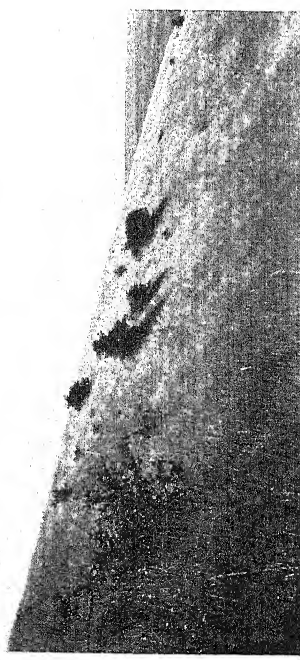


FIG. 2. North escarpment of Beddingham Hill, near Lewes (Area 35), alt. 500 ft. Unpastured grassland with tall *Bromus erectus* and *Avena pratensis* dominant. *Pimpinella saxifraga* in flower (left foreground). Scattered bushes of *Crataegus* (Eastern Downs).

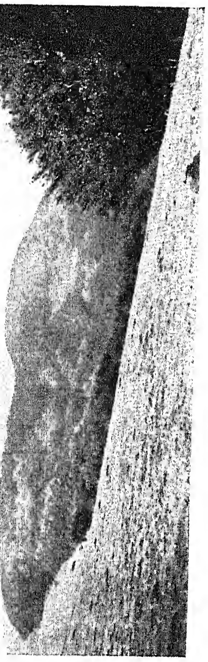


FIG. 3. Pastured chalk grassland at summit (600–700 ft.) of North escarpment, the slope of which is occupied by (probably) natural beechwood. Chanctonbury Ring (planted) in the distance (West-Central Downs).

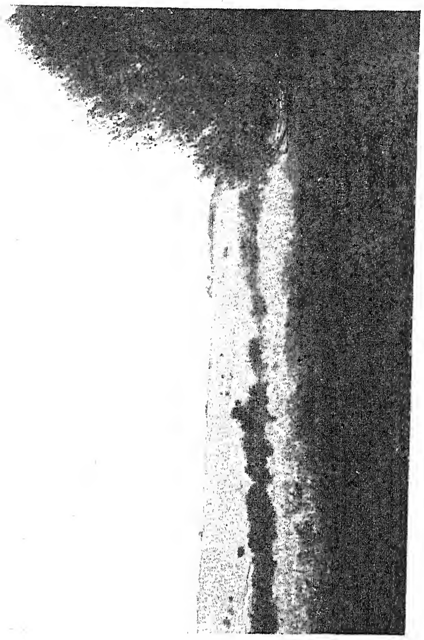


FIG. 4. Heath on chalk plateau (Area *b*), alt. 400 ft. The dark vegetation in front is *Erica cinerea*, the light strip *Brachypodium pinnatum*, the darker strip behind *Ulex nanus*. *Ilex aquifolium* on the right. South of "No Man's Land," near Steyning (West-Central Downs).

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D. Isolated Downs East of Lewes.

30. *Mount Caburn.* Slope 23–28° S., alt. 300–400 feet. Herbage 4 to 6 in., rather sparse. *Bromus erectus* and *Avena pratensis* dominant: these two, with *Poterium sanguisorba*, make up the great bulk of the herbage. A poor list of species and very few mosses: no bushes. Soil 2–3 inches to chalk lumps. Dries blackish, soft—many shells. Considerable carbonate and high organic content in surface layers.

31. *Mount Caburn.* Slope 23–25° N., alt. 400 feet. Herbage 8–12 in., much thicker than on (30). *Bromus erectus* dominant, with other grasses and *Poterium*. Other species more numerous and the Hylocomia present. One or two *Crataegus* bushes. Soil similar to (30), 2 to 3 inches to big chalk lumps.

32. *Cliffe Hill.* Slope 18° steepening to 32° downwards, S., alt. 200–400 feet. *Bromus erectus* dominant, 9 inch herbage, infl. 30 in. (very dry season of 1921 herbage 4–6 in., infl. 24 in.). On the steepest slope ridges a few inches apart, dominated by *Bromus erectus*, follow the contour lines of the hill: between these the sheep walk and browse on the turf, which shows bare chalky soil here and there. They avoid the *Bromus* on the whole (according to a shepherd they only eat the ripe seed) but here and there young *Bromus* shoots were seen eaten off. (Cf. Perching Hill, 22.) At the slope of 18° turf just continuous: large chalk lumps met with in soil at 3 inches' depth. *Crataegus* rare.

33. *Malling Hill.* Flat top, alt. 450 feet. Typical chalk flora: no alien elements. *Festuca ovina* dominant. Herbage short, pastured. Soil blackish, shrinks in drying: 4 in. to chalk, reaction neutral, high organic but low carbonate content.

E. Eastern Downs (Firle Region).

34. *Itford Hill.* Slope 10–15° S., alt. 200–300 feet. Herbage short, pastured. Typical chalk pasture flora. Soil 3 inches to chalk, brown, moderate organic and carbonate content, reaction distinctly alkaline.

35. *Beddingham Hill.* Slope 35° to N.E., alt. 400–500 feet. (Pl. I, fig. 2.) Herbage 12 in. Grass inflorescences 36 to 42 in. *Bromus erectus* dominant, other tall grasses and many other species associated. Mosses, mainly Hylocomia and *Brachythecium purum*, form a continuous stratum. Soil more than 12 inches deep. A few chalk lumps at 10–12 in. Top 4 inches with the greatest mass of roots, reaction alkaline, light grey in colour—low organic content. Seedling *Fraxinus*. Occasional plants of *Ulex europaeus*, *Rubus leucostachys*, *R. rusticanus*, *Solanum dulcamara*.

36. *Firle Beacon.* Slope 30–32° N., alt. 600–700 feet. Herbage 12 in., a mixture of tall grasses, locally eaten down by sheep. *Brachypodium pinnatum* dominant over many acres of the scarp: sometimes burned over since sheep refuse it. The *Brachypodium* shoots freely after burning, and *Pimpinella*, *Leontodon hispidus*, with *Sonchus oleraceus* and other weeds, grow between the shoots. Mosses locally abundant. Soil 3 in. of loam to disintegrated chalk.

F. Extreme Eastern Downs.

37. *Beachy Head.* Slope 20–24° to S.E. (¼ mile from the sea), alt. 200–300 feet. Parallel ridges following the contours as in (33), turf very short between. Herbage ½ to 6 in. Typical chalk grassland showing no maritime influence except possibly the frequency of *Daucus carota*. *Poterium sanguisorba* and *Galium verum* bulk conspicuously. Patches of scrub with *Ulex europaeus*, *Rubus rusticanus*, *Sambucus nigra*, *Prunus spinosa*, *Crataegus*, and *Rosa* spp., also *Teucrium scorodonia*, *Inula squarrosa* and *Brachypodium silvaticum*. Soil 2 inches of brown loam, grey below this. Chalk lumps at 5 inches.

38. *Beachy Head.* Flat top of cliff, alt. 500 feet. Turf very short, no tall grasses except in local shelter. Soil, locally 6 inches of brown loam with no chalk lumps: in other places chalk lumps are met with an inch or two from surface and the chalk *in situ* is at 5 in.

39. *Exceat.* Slope 5° W. on east side of Cuckmere valley one mile from the sea, alt. 50 feet. Soil alkaline, 4 inches to chalk. Poor flora, no mosses.

40. *Cliff End.* Top of cliff, alt. 200 feet, flat, some distance from edge. Herbage ½ inch. Soil alkaline, six inches to chalk. Poor flora, no mosses.

41. *South Hill,* just west of Cuckmere Haven, alt. 150 feet. Herbage 3–4 inches, inflorescences 9–10 inches. Soil a friable loam more than 12 inches deep, moderate to strong effervescence with HCl. The top 4 inches showed the most alkaline reaction met with, pH 8·2.

Notes on the Vegetation and Flora of the Maritime Region of the Sussex Chalk.

The last five areas listed (37–41) were all fairly close to the sea (within ¼ mile except 39 which was 1 mile). The maritime influence was not, however, marked except in two negative points—the general poverty of the flora and the almost complete absence of mosses. 37, in a sheltered hollow on the east side of Beachy Head, alone had a fairly long list of species, but even here *Brachythecium purum* was the only moss seen.

The following general notes on the vegetation of this tract of country between Beachy Head and Seaford are added.

The turf on the top of the cliff edge between Beachy Head and Belle Tout (alt. 300 feet) is very short (½ inch), due probably in the first place to full exposure to violent winds as well as to the sun, partly perhaps to trampling. That exposure is probably the main cause is indicated by the occurrence on the sides of trenches which were dug during the war of *Teucrium scorodonia*, *Clinopodium vulgare*, etc., and the growing up of the grasses in the slightest hollow where they obtain local shelter. The general turf consists of a mixture of the commonest of the more "xerophilous" chalk grassland grasses and herbs, such as *Festuca ovina*, *Briza media*, *Cirsium acaule*, *Plantago media*, *Carex flacca*, with *Cynosurus cristatus*, *Poterium sanguisorba*, *Lotus corniculatus*, etc. There are patches of *Brachypodium pinnatum*, which suffers much, however, from exposure and trampling. The "sub-maritimes" *Erodium cicutarium* and *Plantago coronopus* were first seen here. The soil is very variable, with frequent patches of clay-with-flints passing down into soil with chalk lumps, the chalk rock lying in some cases at a considerable depth (e.g. over 6 feet).

From Belle Tout to Birling Gap and beyond to the Cuckmere valley there is a very mixed vegetation, the edaphic, biotic and local climatic conditions varying very much from place to place. There are patches of *Ulex europaeus*, the leading shrub on all this range of cliffs, often planted for cover, often burned over, and a good proportion shooting from the base of the burned

stems. *Reseda lutea* colonises the burned ground abundantly: also *R. luteola* and *Echium vulgare*. The soft young shoots of *Ulex* are much rabbit eaten. *Calluna*, *Erythraea* and *Euphrasia* are also conspicuous here. Inland the plateau is largely covered by windswept *Ulex*. *Ligustrum vulgare*, badly wind-cut, but growing vigorously, occurs, also the submaritime *Agropyrum pungens*.

On the top of "Seven Sisters" cliffs the intervals between the patches of *Ulex* in the hollows are filled with *Brachypodium pinnatum* which thus obtains partial shelter. In another hollow *Brachypodium* and *Bromus erectus* mixed (with some *Dactylis glomerata* and *Festuca rubra*) alternated with *Ulex*.

On the cliff in more than one place there occurred a well marked semi-open community of the following plants extending only three or four yards from the edge on four inches of soil mixed with chalk lumps under the most extreme conditions of exposure.

Bromus mollis *forma* (? nanus) dominant	
Echium vulgare	Thymus serpyllum
Sedum acre	Plantago media
Hieracium pilosella	Anthyllis vulneraria
Poterium sanguisorba	Reseda lutea
Senecio campestris	R. luteola
Festuca ovina	Glaucium luteum
Cirsium arvense	Arenaria serpyllifolia
Euphorbia exigua	Cerastium tetrandrum
Bellis perennis	Hippocrepis comosa

[The following maritime and submaritime plants were met with on the tops of the cliffs (100 to 200 feet) between Beachy Head and Seaford.

Agropyrum pungens	Erodium cicutarium
Armeria maritima	Glaucium luteum
Carduus pycnocephalus	Plantago coronopus

Daucus carota is locally very abundant, far more so than on any inland area examined.

On a ledge of cliff 10 feet above the beach at Cliff End (Cuckmere Haven) were *Statice limonium*, *Glyceria maritima* and *Spergularia marginata*: a little lower down *Obione portulacoides*, *Beta maritima* and *Crithmum maritimum*. These formed definite local communities (Moss's "association of spray-washed rocks").]

G. "CHALK HEATHS" AND HEATHS.

The areas on which *Calluna* or *Erica cinerea* is developed (with the single exception of 15) have been excluded from Table I, and are separately listed in Table II. That no sharp line can be drawn between chalk heath and chalk grassland would be expected, and there are in fact all transitions from pure chalk grassland to typical "chalk heath" (perhaps also from this to true heath, though this point has not been studied). While such plants as *Sieglingia decumbens*, *Agrostis tenuis* and *Potentilla erecta* may occasionally be found in good chalk grassland such as is developed on fairly steep slopes or on narrow ridges, it is apparently the rule that on very gentle slopes and flat surfaces, *Calluna* eventually appears and the other species mentioned increase in abundance, though most of the chalk grassland plants normally remain, as is shown clearly enough by the fact that the general list of species in Table II differs very little from that in Table I. This gives the mixed community which has been called a "chalk heath." Whether it would normally develop into a true heath with elimination of the characteristic chalk grassland plants is a question that has not been investigated. The pH determinations made on the soil samples collected are below pH 7 in the top layer of soil of the four "chalk

heaths" given in Table II whose soils were tested. In another instance, however (Buddington Farm—see below), the *p*H of the top inch was 7·0.

Chalk heath areas examined (*A*, *B* in well-wooded, *C*, *D* in slightly-wooded, *E*, *F* in non-wooded region).

A. *Heyshott Down*. Summit, flat, 700 feet. At the highest level of the summit there was a vegetation of *Calluna* (v.a. to d.) with *Dicranum scoparium* and *Agrostis tenuis* on 4 inches of loam with a *p*H value of 6·9. Below this were flints and then (5–9 in.) flints mixed with disintegrated chalk lumps to chalk *in situ* at 9 inches. Isolated bushes of *Crataegus*, *Rubus idaeus* and *Rubus* sp.

At a slightly lower level but still on the flat summit of the Down was a vegetation composed mainly of the common chalk grassland plants, but with *Potentilla erecta*, *Luzula campestris*, *Dicranum* and *Cladonia* conspicuous. The turf was half an inch deep with two inches of soil, then three inches with numerous small chalk lumps, and chalk *in situ* at five inches.

B. *Burton Down*. Summit, flat to 10° S., close to woodland, alt. 700 feet. Turf very badly rabbit eaten, ¼ inch, of *Festuca ovina-Agrostis tenuis*; only where mosses (*Hylocomia*, *Dicranum*, etc.) occurred was there a herbage depth of two inches. The clumps of *Calluna* were severely eaten back. A little distance away *Calluna* was less eaten 12–18 in. high, flowering. Scattered *Ulex europaeus*, *Crataegus*, *Rosa lutetiana*, *Rosa* sp. and *Fraxinus*. Soil 4 in. of brown loam, then 6 inches with flints and 2 inches with chalk lumps. Chalk *in situ* at 12 inches. (On east slope stiff yellow clay with flints to at least two feet.)

C. *Plateau between Steyning Round Hill and No Man's Land*. Alt. 500 feet. Light brown very friable dry loam mixed with flints and a few very small chalk fragments. Practically uniform to 16 inches (chalk *in situ*). Roots abundant to 4 inches, still frequent at 12 inches, some penetrating to chalk. Bushes of *Crataegus*, *Juniperus*, *Rubus leucostachys*, *Prunus spinosa*. Mosses generally absent (*Brachythecium rutabulum* local).

This is not a chalk heath; on the contrary it has a *p*H value of 7·4, and none of the chalk heath plants except *Agrostis tenuis*, but is included as a flat plateau area for comparison with the others. Possibly it has been ploughed at no distant date.

[On the Chanctonbury plateau, east of Buddington Farm at an altitude of 600 feet there is good chalk heath with the following species on the comparatively shallow soil (7 inches) overlying the chalk:

Calluna vulgaris	co-d.	Hieracium pilosella	f.
Festuca ovina	co-d.	Lotus corniculatus	o.
Poterium sanguisorba	a.	Taraxacum erythrospermum	o.
Ranunculus bulbosus	a.	Carex flacca	o.
Cirsium acaule	a.	Potentilla erecta	o.
Plantago lanceolata	f.—a.	Agrostis tenuis	o.
Filipendula hexapetala	f.	Avena pratensis	o.
Thymus serpyllum	f.	Luzula campestris	o.
Veronica officinalis	f.	Achillea millefolium	o.
Leontodon hispidus	f.	Trifolium repens	o.
Polygala vulgaris	f.	Linum catharticum	o.

The following are the results of analysis of the 7 inches of soil overlying the chalk:

Depth of sample	pH value	Water loss of air dry soil at 100° C.	Loss on ignition	CaO	MgO	K_2O
0″–1″	7·0	7·5	22·8	1·12	·52	·32
0″–3″	7·2	6·7	18·9	·74	·53	·31
3″–7″	7·5	6·3	16·0	·78	·58	·28

On the adjoining plateau *Calluna* and *Helianthemum* together occupied many mole heaps.]

D. Mount Harry. Flat top, alt. 600 feet. Variable short turf (½–4 in.) cattle pastured and some rabbits, with *Calluna*, *Agrostis tenuis*, *Sieglingia decumbens* and *Potentilla erecta*, and also a number of ordinary chalk grassland plants: occasional bushes of *Ulex europaeus* and *Crataegus*, *Fraxinus* seedling. Soil 4 inches of dark humous loam with a few flints, shrinking to a cake on air drying, overlying chalk at 4 inches. Surface 2 inches markedly acid (pH 6·0 to 6·5), rich in organic matter and poor in carbonates.

E. Beddingham Hill plateau. Alt. 600 feet. Grasses and clovers conspicuous, the Avenae and *Bromus erectus* absent. *Calluna* (and elsewhere *Erica cinerea*) abundant locally. *Ulex europaeus* and *Rubus* spp., *Mespilus germanica* in scrub. Soil 3 inches of loam, then flints to over 8 inches from surface.

F. Firle Beacon plateau, close to edge of escarpment. Alt. 700 feet. Good chalk heath. Soil 6 inches of sandy loam, pH 6·9.

The plateau and dipslope ridges running south from the Firle Beacon massif are largely covered with loam and flints and bear rough scrub in which *Rubus* spp. and *Ulex europaeus* are prominent, with *Calluna* and *Erica cinerea* alternating. *Ulex nanus* (*minor*) occurs among the *Calluna*. There is also a great deal of *Brachypodium pinnatum* in patches. Arable land alternates with the waste, and from this *Cirsium arvense* often invades. The whole region is very similar to the Chanctonbury-Cissbury region 22 miles to the west.

Three-quarters of a mile to the south-east of area F *Calluna* (in isolated tufts, eaten back) gets 40 yards down over the edge of the plateau in the closely eaten turf of the escarpment slope at an angle of 20°. This is the maximum angle of chalk slope on which *Calluna* has been found.

Heaths. Two areas which may fairly be called "heaths" without the prefix "chalk" were listed—the summit of Graffham Down in the well-wooded western area, and an area south of "No Man's Land" on the Chanctonbury-Cissbury plateau. Both of these show relatively high acidities, values below pH 6, and an absence of many of the chalk grassland plants.

a. Graffham Down. Flat, on the plateau close to the top of the escarpment, alt. 700 feet, in an angle of forest. Here *Erica cinerea* is abundant to dominant and *Calluna vulgaris* locally abundant. But between these dwarf shrubs there are patches of rabbit-eaten turf. There is an abundance of scattered

bushes and young trees, the area clearly being on the way to develop forest. The following woody plants occurred:

Cornus sanguinea	Lonicera periclymenum	Salix cinerea
Crataegus monogyna	Prunus spinosa	Sorbus aria
Fagus silvatica	Rosa micrantha	Ulex europaeus
Fraxinus excelsior	Rubus leucostachys	Viburnum lantana
Ligustrum vulgare		

There is a long list of herbaceous plants—a mixture of chalk grassland and heath species, with a few woodland forms: namely, *Digitalis purpurea*, *Dryopteris filix-mas*, *Epilobium angustifolium*, *Potentilla sterilis*. The last named are omitted from the list in Table II.

Though Graffham Down summit is on the whole a heath, it contains a certain admixture of chalk grassland elements. The soil is a dry light loam mixed with flints. The top 4 inches are very poor in carbonates and the *p*H value obtained was 5·8. There is no visible sign of chalk to a depth of one foot, but at this level chalk lumps occur.

b. Heath south of "No Man's Land" (Chanctonbury). Alt. 400 feet, slope 5° to S.E. (Pl. I, fig. 4.) This area was dominated by alternating patches of *Erica cinerea* with *Ulex nanus* and patches of *Brachypodium pinnatum*: scattered bushes of *Crataegus*, *Sambucus nigra*, *Ulex europaeus*, *Rubus caesius*, *R. leucostachys*, *R. rusticanus*, *Rosa canina*, *Ilex* and *Fraxinus*, with *Clematis vitalba*. Soil a light-brown dry friable loam inclined to be clayey at 6 in.: at 8 inches a few flint fragments. The *p*H value of the top 8 inches was 4·6.

In comparing the lists from these chalk-heath and heath areas with those from the chalk grasslands we see that the occurrences and abundance of such characteristic chalk grassland species as the Avenae, *Bromus erectus*, *Koeleria gracilis*, *Scabiosa columbaria*, *Pimpinella saxifraga*, *Phyteuma orbiculare*, are more or less diminished on the chalk heaths, while all these except *Pimpinella* are quite absent from the heaths, as well as *Linum catharticum* and *Bellis perennis*. On the other hand, in addition to the appearance of *Calluna*, there are increased occurrences and abundance on the chalk heaths of *Agrostis tenuis*, *Carex caryophyllea*, *Holcus lanatus* (to some extent) and *Sieglingia decumbens*.

On the heaths appear, besides *Calluna* and *Erica*, *Carex pilulifera*, *Hypericum pulchrum*, *Hypochaeris radicata* (found in only one of the 41 grassland areas), *Stachys betonica*, *Galium saxatile*, *Ceratodon purpureus*. *Polytrichum juniperinum* and *Hypnum cupressiforme* var. *ericetorum*, too, appear on the heaths and on one of the chalk heaths.

But the great majority of all the species are common to the three communities. It is clear that the chalk heath cannot be regarded as more than a modification of chalk grassland in the direction of heath, while the two genuine heaths on the chalk plateau have a poor list of heath species. They may be regarded as "association-fragments" in the sense of the Upsala and new Zürich schools, strongly influenced by the flora of the surrounding chalk grassland. It is only locally that the "leaching" plateau succession has developed heath.

3. FLORA AND SOILS OF THE AREAS

The two following tables (pp. 16–23) record the data collected.

4. SOILS OF CHALK GRASSLAND

The areas of chalk grassland from which the data presented in this paper are taken were all situated, as already mentioned, on comparatively shallow soils overlying and obviously directly derived from the chalk itself. Small single samples of the soil were taken from a majority of these areas (in three cases two samples from each) and the results of the partial analyses of these are given in Table I. Nearly all the samples were taken from the layer of maximum root development: the actual depths are given in the table. Such data are of course quite inadequate as the basis of a general account of the chalk grassland soils as such, but some comparative remarks may suitably be made here.

Broadly speaking three types of soil were met with: (1) a *grey powdery soil* with a very high calcium content, and varying in tint according to the humus content, which was often high, (2) a *brown loam*, also with a high average humus content, and (3) a *dark coloured sometimes black soil*, very rich in humus and shrinking to a tough compact cake on drying. Of these (2) is the commonest and (1) the rarest, (3) occurring exclusively, in our experience, on steep northern escarpment slopes bearing tall herbage. In one or two cases a grey soil occurred under tall herbage. This may very well be due to intermittent heavy grazing checking the accumulation of humus, but the point could not be determined without far more field study than we could give.

	CaO		Loss on ignition		*p*H	
	Average	Range	Average	Range	Average	Range
(1) 6 grey soils	29·1	21·7–37·9	24·6	11·6–31·6	7·4	6·5–7·9
(2) 6 brown soils	18·1	9·3–27·4	25·9	20·5–32·7	7·4	6·9–7·6
(3) 7 dark soils	15·0	2·4–25·8	31·3	23·5–42·6	7·5	7·2–7·8

It is clear that the grey soil is the most primitive, though the areas examined, all of which bore pretty fully developed chalk pasture, are none of them so primitive as the Buriton Limeworks (*a*) soil (see No. III of these "Studies," This JOURNAL, **13**, p. 184), which contained far more calcium and far less humus than any of those considered in the present paper. Transitional soils between (1) and (2), grey-brown in colour, were met with, and also between (1) and (3), blackish-grey. These last dried black, or nearly black, but soft and powdery, while the typical dark humous soils (3) dried into a tough black or dark brown cake with considerable shrinkage.

It seems, therefore, that while the dark humous soils (3) are derived from (1) under conditions of moisture and rank growth of herbage, the brown soils (2) are formed from (1) under conditions of pasturage, and greater dryness. These brown soils are the most widespread and occur on medium and also

Table I.

		Extreme W.		Western Downs (mainly wooded) (Cocking gap to River Arun)							West-central Downs (River Arun to River Adur)								
Aspect ……		E.	E.	N.N.W.	N.	W.	E.	S.	S.	N.	W.	W.N.W.	N.	N.	N.W.	N.	N.	N.	S.E.
Slope …….		24–35°	16°	18–20°	32°	10°	10–12°	22°					18–32°	22–32°	32–37°	15°	27°	27°	5°
	Life-form	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Aceras anthropophora	G	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Achillea millefolium	H	f.	o.	—	o.–f.	f.–a.	—	o.	o.	—	o.	—	o.	f.	f.	o.–f.	f.	f.	—
Agrimonia eupatorium	H	r.	—	—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—	o.
Agrostis alba	H	—	o.	o.	f.–a.	o.–f.	f.	—	—	—	a.	f.	o.	—	a.	o.	—	l.a.	a.
A. tenuis (vulgaris)	H	l.a.	a.	—	—	o.	—	—	—	o.–f.	—	—	—	—	—	a.	—	—	—
Anthoxanthum odoratum	H	f.	o.	—	—	f.	f.	—	—	f.	a.	f.	f.	o.	o.	a.	f.	—	—
Anthriscus silvestris	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Anthyllis vulneraria	H	l.a.	—	—	—	—	f.	—	—	—	—	—	—	—	—	—	—	—	r.
Arabis hirsuta	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arenaria serpyllifolia	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arrhenatherum elatius	H	—	—	—	—	—	—	—	—	—	l.	l.	—	—	l.	—	—	l.a.	l.
Asperula cynanchica	Ch	f.	f.–a.	f.	f.	f.	f.	o.–f.	o.	f.	f.	f.	o.	o.	o.	o.	f.	o.	l.a.
Avena pratensis	H	l.a.	l.	o.	—	f.–a.	f.	f.–a.	o.	o.	a.	l.a.	l.	l.a.	v.a.	o.	o.–f.	a.	a.
A. pubescens	H	l.a.	—	l.	l.	f.–a.	f.	—	—	f.–a.	f.	f.	o.	—	—	o.	o.–f.	l.a.	—
Blackstonia perfoliata	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bartsia odontites	Th	—	—	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	r.
Bellis perennis	H	o.	o.	o.	o.	o.	o.–f.	—	o.	o.	o.	o.	o.	o.	—	o.	o.–f.	—	f.
Brachypodium pinnatum	H or Ch[1]	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.d.	l.
B. silvaticum	H	—	—	l.	—	—	—	l.	—	—	—	—	—	—	—	—	l.	—	—
Briza media	H	f.	o.	o.–f.	f.	f.	a.	f.	f.	o.	f.–a.	f.	f.	o.–f.	f.	o.	f.	f.	—
Bromus erectus	H	l.	—	—	—	l.	o.	—	—	—	l.	l.	—	—	l.	—	—	d.	l.
B. mollis	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Calluna vulgaris	Ch	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—	—	—
Campanula glomerata	H	o.	—	o.	—	o.	f.	—	—	—	—	—	r.	—	—	—	—	—	—
C. rotundifolia	H	f.–a.	o.–f.	f.	f.	f.	f.	l.a.	o.	—	f.	f.	o.	f.	o.	f.	f.	f.	o.
Carex caryophyllea	G	o.	o.	f.	o.–f.	—	o.–f.	—	—	f.	o.	f.	o.	o.	—	o.	f.	—	—
Carex flacca (glauca)	G	a.	v.a.	v.a.	a.	f.	f.–a.	v.a.	v.a.	a.	o.–f.	f.–a.	a.	a.	f.	f.	v.a.–c.d.	a.	r.
Carlina vulgaris	H	o.	o.	o.	—	—	o.	o.	—	r.	—	o.	—	o.	—	o.	o.	—	f.–l.a
Caucalis anthriscus	H	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	—	—	—	—
Centaurea nigra	H	l.	—	o.–f.	—	a.	—	—	—	—	—	o.	f.	o.	o.	—	—	o.	o.
C. scabiosa	H	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—
Cerastium vulgatum	Ch	l.	o.	—	—	l.	—	—	—	—	—	—	—	—	r.	—	f.	—	—
Cirsium acaule	H	f.–a.	f.–v.a.	a.	a.	f.–a.	a.–v.a.	v.a.	v.a.	a.	f.	a.	a.	a.	a.	f.	f.–l.a.	o.–f.	f.
C. arvense	G	—	—	—	—	—	—	r.	a.	—	—	—	—	l.	—	—	—	—	o.
C. lanceolatum	H	r.	r.	—	—	r.	—	—	—	—	—	—	—	l.	—	—	—	—	o.
C. palustre	H	—	—	—	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	o.
Clinopodium vulgare	H	l.	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Crepis virens	Th	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	f.
Cynoglossum officinale	H	l.	—	—	—	—	—	—	—	r.	—	—	—	—	—	—	—	—	—
Cynosurus cristatus	H	—	a.	—	—	o.–f.	o.–f.	l.	—	—	f.	—	—	—	l.	—	o.	—	f.
Dactylis glomerata	H or Ch[1]	l.	l.	—	—	o.–f.	o.	—	—	—	l.a.	l.	l.	l.a.	a.	—	l.a.	a.	f.–a.
Daucus carota	H	o.	—	o.	—	r.	—	o.	—	—	l.	—	—	—	—	—	—	—	f.
Deschampsia caespitosa	H or Ch[1]	—	—	—	—	—	—	—	—	—	—	—	—	—	f.	—	—	l.	—
Echium vulgare	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Erythraea centaurium	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Euphrasia nemorosa	Th	o.	o.–f.	f.	f.	o.	r.–o.	f.–a.	o.–f.	—	—	o.	f.	—	—	f.	o.	o.	o.
Festuca elatior	H or Ch[1]	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—	—	—
F. ovina	H	v.a.	v.a.–d.	f.–a.	a.	a.	f.	v.a.	v.a.–d.	d.	v.a.	a.	v.a.	v.a.	a.	v.a.	v.a.	a.–s.d.	v.a.
F. rubra	H	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	l.a.
Filipendula hexapetala	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	f.	l.	—	—
Fragaria vesca	H	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	—
Galium erectum	H	l.	l.	—	o.	—	—	—	—	—	—	—	l.	l.	o.	—	o.	—	—
G. mollugo	H	r.	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—
G. verum	H	a.	o.	—	—	f.	f.	—	—	f.	o.	o.	o.–f.	—	l.	f.	o.	f.	l.a.
Gymnadenia conopsea	G	—	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—

[1] These tufted grasses, though classed by Raunkiaer as hemicryptophytes, may, in our climate, have perennating buds above the soil surface.

Table I.

East-central Downs (River Adur to River Ouse)											Mount Caburn group east of Lewes				Eastern Downs								Occurrences	
															Firle region			Maritime region extreme east						
N. 15–25°	N. 30–32°	N. 30–35°	N. 32–37°	N. 37–40°	N. 22–24°	N.N.W. 30°	S.S.E. 30°	N. 35–37°	N. 30°	N. 30°	S. 23–28°	N. 23°	S. 18–32°	Flat	S. 10–15°	N. 30°	N. 30–32°	S.E. 20–24°	Flat	W. 5°	Flat	S.	No. of areas	%
19	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**		
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
a.–l.v.a.	f.	f.	f.	—	f.–a.	o.–f.	—	f.	a.	o.	—	f.	o.	o.	o.	f.	f.	f.	f.	—	—	l.a.	31	76
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	4	10
f.	o.	—	l.a.	—	a.	—	—	f.	a.	l.a.	—	—	—	—	—	f.	l.a.	f.	—	—	—	—	22	54
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	12
v.a.	a.	f.	f.	a.	l.v.a.	f.	—	a.. l.d.	l.a.	f.	—	l.	f.	o.	—	f.	—	f.	o.	—	—	—	28	70
—	—	—	—	—	—	—	—	r., l.	—	—	—	—	—	—	—	—	r., l.	—	—	—	—	—	2	5
l.a.	—	—	—	—	—	—	—	—	—	—	l.a.	o.	o.	o.–f.	f.	—	—	l.f.	—	—	o.	o.	12	30
—	—	—	—	—	o.	r.	—	o.	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	4	10
—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	o.	—	—	—	—	—	—	—	2	5
l.	—	—	—	—	—	—	—	l.v.a.	—	—	—	l.	—	—	—	l.	—	—	—	—	—	—	9	22
o.	f.	—	o.	f.	f.	—	—	—	—	a.	f.	a.	a.	—	—	a.	l.a.	a.	a.	—	—	—	31	76
v.a.–d.	v.a.	o.	v.a.	v.a.	a.	a.	a.	v.a., l.d.	l.v.a.	v.a.	a.	a.	a.	o.	o.	a.	l.a.	l.a.	a.	f.	—	v.a.–c.d.	39	95
a.	a.	v.a.	—	f.	v.a.–d.	a.	—	a.	d.	o.	a.	a.	a.	r.–o.	l.f.	f.	o.	—	—	—	—	—	28	70
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
—	—	l.	l.f.	—	o.–f.	—	—	—	—	—	—	—	f.	f.–a.	o.	o.	o.	—	o.	o.	o.	—	26	65
o., l.d.	—	o.	—	—	r.	—	—	—	—	o.	—	—	l.	—	—	—	l.d.	—	—	—	—	—	8	20
—	—	—	—	r.	—	—	—	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	5	12
a.	a.	o.	f.	r.	f.	f.–a.	f.	f.	l.	a.	—	o.–f.	f.	o.–f.	f.	f.	f.	f.	f.	f.	a.	a.	39	95
l.a.–l.d.	l.a.	—	—	r.	l.	—	—	l.a.	l.v.a.	l.	d.	d.	d.	f.	l.	d.	l.	—	r.	d.	f.	—	25	62
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	12
f.	a.	—	o.	o.	o.	—	—	—	f.	f.	o.	—	f.	—	—	o.	—	—	—	—	—	—	27	67
—	—	—	f.	—	o.	—	r.–o.	r.	—	f.	o.	—	o.	o.	—	o.	—	—	—	—	—	—	21	52
o.	a.	o., l.	v.a.	a.	f.	f.	a., l.v.a.	l.a.	o.	a.	r.–o.	f.	a.	a.	v.a.	a.	f.	a.	a.	o.	a.	a.	41	100
—	o.	—	—	o.	o.	—	r.–o.	—	—	r.	o.–f.	—	f.	—	—	o.	o.	o.	r.	—	—	—	22	54
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	—	—	—	—	2	5
o.–f.	o.	o.	o.	l.	o.	o.	—	a.	a.	r.	o.	o.	o.	—	—	f.	o.	f.	l.f.	—	—	a.	27	67
—	—	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
r.	—	o.–f.	—	—	o.	—	—	f.	r.	o.	r.	o.	—	f.	—	—	o.	—	—	—	—	—	15	45
f.	o.	o.	f.	f.	f.	o.	a, l.d.	—	l.a.	o.–f.	a.	o.l.	f.–a.	f.–l.d.	f.	f.	a.	f.	f.	f.	o.	a.	40	98
—	—	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	r.	l.	r.	—	—	a.	l.	11	27
—	—	—	—	—	—	—	—	r.	—	—	—	—	—	—	—	—	o.	—	—	—	—	—	7	17
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
—	—	—	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	3	7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.	o.	—	—	—	—	4	10
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
l.	l.	—	f.	—	f.	—	—	—	—	—	—	—	—	—	o.	—	—	—	f.	o.	—	—	15	37
l.a.	f.	v.a.	a.	f.	f.–l.d.	l.	r.	f.–a.	f.	f.–l.a.	—	f.	l.	—	—	f.	f.	l.	—	—	—	f.	29	72
—	—	—	—	—	o.	—	f.	—	—	—	—	o.	o.	o.	—	—	—	f.	—	o.	o.	a.	15	37
l.	l.a.	o.	a.	l.	l.	—	—	a.	l.v.a.	l.	—	—	—	—	—	o.	l.	—	—	—	—	—	13	32
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.	r.	—	—	—	2	5
—	o.	—	o.	o.	o.	—	f.	—	—	—	—	—	—	—	—	o.	o.	f.	—	o.	—	o.	24	60
l.	—	—	—	—	—	—	—	l.d.	l.v.a.	—	—	—	—	—	—	—	—	—	—	—	—	o.	4	10
f.	v.a.	o., l.	v.a.	v.a.	—	a.	a.	l.a.	o.	v.a.–l.d.	f.	o.	f.–l.a.	v.a.–d.	v.a.	f.	l.a.	v.a.	v.a.	f.	a.	—	39	95
f.	—	f.	—	—	f.–a.	—	—	—	—	o.	—	—	—	—	—	—	—	—	l.	—	—	v.a.–c.d.	8	20
o.–f.	—	—	—	—	—	—	o.	—	—	—	o.–f.	o.	f.–v.a.	o.	a.	—	—	l.f.	l.a.	f.	—	l.a.	13	32
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
o.	o.	f.	—	o.	—	—	—	f., l.a.	f.	l.	—	f.	—	—	—	l.	o.	o.	—	—	—	—	18	45
—	—	—	—	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7
f.	l.a.	—	o.–f.	l.	o.–f.	—	—	a.	—	l.a.	—	o.	l.a.	—	—	o.	l.a.	a.	f.	—	—	—	26	65
o.	—	—	—	—	—	—	—	—	—	—	—	l.f.	—	—	—	—	—	—	—	—	—	—	3	7

Table I (*contd.*).

		Extreme W.		Western Downs (mainly wooded) (Cocking gap to River Arun)							West-central Downs (River Arun to River Adur)								
Aspect ……		E.	E.	N.N.W.	N.	W.	E.	S.	S.	N.	W.	W.N.W.	N.	N.	N.W.	N.	N.	N.	S.E.
Slope ……		24–35°	16°	18–20°	32°	10°	10–12°	22°					18–32°	22–32°	32–37°	15°	27°	27°	5°
	Life-form	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Gentiana amarella	Th	o.	r.–o.	o.	o.	o.–f.	o.	—	—	o.	—	o.	o.	o.	—	o.	o.	—	—
Habenaria viridis	G	—	—	—	—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—
Helianthemum vulgare	Ch	—	—	o.–l.d.	—	l.	—	o.–f.	—	—	—	—	l.	—	—	l.	—	—	—
Hieracium pilosella	H	l.a.	l.a.	f.–l.d.	o.	o.	o.	f.–v.a.	v.a.	o.	f.	f.–a.	l.f.	o.	—	o.–f.	f.–a.	—	l.a.
Hippocrepis comosa	H	—	—	a.–l.d.	—	—	—	—	—	—	—	—	—	—	—	—	l.	—	—
Holcus lanatus	H	—	—	—	—	l.a.	l.	—	—	l.	o., l.	—	l.	l.	—	l.	—	—	o.
Hypericum perforatum	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hypochaeris radicata	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.
Koeleria gracilis	H	f.	—	o.–f.	o.	o.–f.	f.–a.	o.–f.	o.–f.	—	f.	l.f.	—	l.	o.	f.	o.–f.	o.	f.
Lathyrus pratensis	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leontodon autumnalis	H	o.	o.–a.	f.	o.	—	o.	—	—	o.	o.	—	o.	o.	—	o.	—	—	f.
L. hispidus	H	a.	f.–a.	f.–a.	l.a.	f.	f.–a.	v.a.	f.	o.–f.	o.–f.	f.	a.	f.	o.	o.	f.	o.	o.
Leucanthemum vulgare	H	o.	—	—	—	—	o.	—	—	—	—	—	o.	o.	—	—	o.	—	—
Linum angustifolium	Th or H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
L. catharticum	Th	o.	o.–f.	f.–a.	f.	f.	o.–a.	f.–a.	o.	f.	o.	f.	f.	f.	—	o.–f.	f.–a.	o.	f.
Listera ovata	G	—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lolium perenne	H	—	l.	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	—
Lotus corniculatus	H	a.	a.	f.	f.	f.–a.	f.	f.–a.	a.	f.	f.	a.	o.	f.	a.	f.	a.	a.	a.
Luzula campestris	H	—	—	—	—	o.	—	—	—	o.	—	—	—	—	—	—	o.	—	—
Medicago lupulina	Th	f.	—	o.	o.	o.	o.–f.	—	o.	—	—	—	f.	o.	o.	—	—	—	a.
Myosotis arvensis	Th	l.	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ononis repens	H	l.f.	—	—	—	—	f., l.d.	—	—	—	—	—	—	—	—	—	—	—	—
Ophrys apifera	G	—	—	—	—	—	r.	o.	—	—	—	—	—	—	—	—	—	—	—
Orchis maculata	G	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—
O. pyramidalis	G.	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Origanum vulgare	H	l.	—	—	—	l.	l.	o.	—	—	—	—	—	—	—	—	—	—	l.
Phleum pratense	H	l.f.	o.	—	o.	o.	o.	—	—	o.	o.	o.	—	—	—	—	o.	—	f.
Phyteuma orbiculare	H	—	l.	o.	—	r.	o.	o., l.f.	o.	—	—	o.	r.	—	o.	—	o.	f.	—
Picris hieracioides	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.
Pimpinella saxifraga	H	f.	o.	o.	o.	f.	o.	o.	—	—	o.	o.	o.	o.	f.	—	o.	f.	o.
Plantago lanceolata	H	a.	f.–a.	f.	f.	v.a.	f.	f.	o.	f.	f.	f.	a.	f.	f.	a.	a.	a.	f.–a.
P. media	H	o.	l.	o., l.	—	o.–f.	o.–f.	o.–f.	o.	l.	o.	o.	f.	o.	o.	r.	—	—	o.
Poa pratensis	G	—	—	—	—	o.	—	—	—	—	l.	—	—	—	o.	—	—	l.	l.
Polygala vulgaris	H	o.	o.	o.	o.	—	f.	f.	—	—	—	o.	—	—	—	o.	f.	—	—
Potentilla anserina	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.f.
P. erecta	H	—	—	—	—	—	r.	l.	—	—	—	—	—	—	—	f.	—	—	—
P. reptans	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.a.
Poterium sanguisorba	H.	a.–l.v.a.	—	f.	a.	o.–l.v.a.	l.a.	v.a.	—	l.	a.	a.	a.	f.–a.	o.–l.f.	a.	v.a.–c.d.	f.	l.a.
Primula veris	H	l.	r.–o.	l.	r.	o.–f.	f.–a.	o., l.	—	—	—	o.	o.	—	o.	—	l.f.	l.	—
Prunella vulgaris	H	o.	o.–f.	o.	o.–f.	—	o.	—	l.	o.	o.	o.	f.	o.	o.	f.	f.	—	f.
Ranunculus acer	H	—	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	—	—	—
R. bulbosus	H	o.	o.	o.	—	a.	o.–f.	f.	o.	—	—	o.	—	—	o.	—	a.	—	o.
R. repens	H	—	r.	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhinanthus crista-galli	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—
Reseda lutea	Th or H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rumex acetosa	H	—	o.	—	o.	o.–l.a.	—	—	—	—	—	—	—	—	o.	—	o.–f.	r.	—
Scabiosa arvensis	H	o.	—	—	—	r.–o.	—	—	—	—	—	—	—	—	—	—	—	—	—
S. columbaria	H	f.	o.	o.	o.	o.	f.–l.a.	—	o.	—	f.	f.	f.	f.	f.	o.	o.	f.	f.
S. succisa	H	o.	l.a.	—	—	—	—	—	—	—	—	—	o.–f.	—	—	—	—	—	—
Senecio campestris (Cineraria integrifolia)	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. jacobaea	H	r.	o.	—	—	o.	o.	—	—	f.	—	—	—	r.	r.	o.	—	—	—
Sieglingia decumbens	H	—	—	—	—	—	—	l.	—	—	—	—	—	—	—	o.	—	—	—
Sonchus oleraceus	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Spiranthes autumnalis	H	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tamus communis	G	—	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	—	—	—
Taraxacum erythrospermum	H	o.	—	—	—	—	—	o.	—	—	—	—	—	—	—	—	o.	—	—
T. officinale	H	o.	—	—	—	o.	—	—	o.	—	—	—	—	—	—	—	—	r.	—
Thesium linophyllum (humifusum)	G	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thymus serpyllum	Ch	a.	a.	a.	f.–a.	l.	o.–l.f.	o.–a.	f.–a.	f.	o.	a.	f.	o.	o.	f.	a.	o.	a.

Table I (*contd.*).

East-central Downs (River Adur to River Ouse)											Mount Caburn group east of Lewes				Eastern Downs: Firle region			Eastern Downs: Maritime region extreme east					Occurrences	
N. 15–25°	N. 30–32°	N. 30–35°	N. 32–37°	N. 37–40°	N. 22–24°	N.N.W. 30°	S.S.E. 30°	N. 35–37°	N. 30°	N. 30°	S. 23–28°	N. 23°	S. 18–32°	Flat	S. 10–15°	N. 30°	N. 30–32°	S.E. 20–24°	Flat	W. 5°	Flat	S.	No. of areas	%
19	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**		
—	—	—	o.	o.	o.	—	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	—	—	16	40
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
—	—	—	—	—	—	—	f., l.d.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	15
—	—	—	o.	a.	l.a.	—	a.	—	—	—	f.–l.a.	—	f.	a.	f.	l.a.	l.	l.a.	v.a.	a.	a.	o.	31	76
l.d.	—	—	—	—	—	o.	a.–d.	—	—	—	v.a.	f.	l.a.	—	l.a.	l.	l.	l.a.	—	v.a.	—	l.a.	14	35
o.	l.a.	o.	—	l.	l.	—	—	l.a.	a.	l.a.	—	l.	—	—	l.	o., l.a.	—	—	—	—	—	—	19	47
—	—	—	—	l.	—	—	—	l.	—	—	—	l.	—	—	—	—	l.f.	—	—	—	—	—	4	10
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
f.–a.	f.–a.	o.	a.	l.	f.	o.	—	l.a.	o.	a.	—	—	a.	o.–f.	—	f.	l.f.	f.	f.	f.	o.	f.–a.	34	85
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	—	—	—	—	1	2
—	—	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	30
o.	o.	l.	f.	a.	f.	—	a.	—	l.a.	—	o.–f.	a.	f.	—	—	a.	f.–l.a.	f.	f.	—	—	—	33	80
—	—	—	o.	—	—	—	—	—	—	—	—	—	f.	—	—	—	—	—	—	—	—	—	7	17
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.–o.	1	2
o.–f.	f.	l.	f.	f.	f.	o.–l.a.	f.–a.	o.	—	f.–a.	f.–a.	o.	a.	v.a.	v.a.	f.	f.	f.	—	f.	a.	f.	38	93
—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
f.	f.	o.	o.	a.	o.–f.	o.	—	o.	—	a.	—	o.	o.	f.	—	f.	o.	a.	a.	f.	a.	f.	37	90
f.	—	o.	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	15
—	f.	—	f.	—	o.	—	—	—	—	f.	—	l.f.	—	—	—	o.	o.	o.	—	o.	—	o.	20	50
—	—	—	—	—	—	—	—	o., l.	—	l.	—	r.	—	—	—	—	l.f.	—	—	—	—	—	6	15
—	—	—	—	—	—	—	o.	—	—	—	l.a.	—	l.a.	—	—	—	l.	l.a.	—	—	—	—	7	17
—	—	—	—	—	—	—	r.–o.	—	—	—	o., l.	—	—	—	o.	f.	—	—	—	—	—	—	6	15
—	—	—	—	—	o.	—	—	—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—	3	7
r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
—	—	—	—	—	—	—	—	—	—	—	—	o., l.	—	—	—	—	—	—	—	—	—	—	6	15
—	—	—	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	l.	o.	—	—	—	—	13	32
a.	f.	o.	f.	a.	f.	o.–f.	o.	—	—	r.	o.	f.	o.	o.	—	f.	l.	o.	o.	—	—	—	28	70
r.	—	—	—	—	—	—	—	—	—	—	o.	r.	—	—	—	—	—	—	—	—	—	—	4	10
f.	a.	o.	a.	f.	o.–f.	f.	o.–f.	a.	a.	o.	o.	f.–l.a.	f.	f.–a.	—	f.	a.	f.	o.	—	—	—	34	85
f.	a.	f.	f.	o.	f.	o.	f.	a.	a.	f.–a.	f.–a.	f.	f.–a.	f.–a.	f.	f.	f.	a.	a.	f.	f.	f.	41	100
l.f.	—	—	o.	—	o.	—	r.–o.	—	o.	—	o.	—	a.	o.	—	o.	o.	o.	o.	o.	o.	f.	30	74
o.	—	v.a.	—	—	—	—	—	—	o.	—	—	o.	—	—	—	o.	o.	—	—	—	—	—	11	27
l.f.	—	o.	—	—	o., l.	o.	o.–f.	—	—	o.	f.	—	—	r.	o.	—	—	r.	r.	f.	—	o.	22	54
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
v.a.–c.d.	a.	v.a.	f.	f.	a.	a.–l.d.	a.	l.v.a.	a.	a.	a.–v.a.	v.a.	a.	v.a.	v.a.	f.	l.a.	a.	v.a.	a.	a.	v.a.–c.d.	39	95
o.–l.a.	o.	o.	—	—	—	o.	—	o., l.	o.	l.	—	f.	—	—	o., l.	r.	l.	—	—	o.	—	—	24	60
o.	f.	—	f.	f.	f.	—	—	—	a.	f.	—	—	—	—	—	f.	o.	o.	f.	—	—	—	26	65
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
o.	—	o.	o.	—	—	o.	r.	l.f.	—	f.–a.	—	o.	o.	v.a.	a.	o.	—	—	—	o.	l.	f.	26	65
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
—	—	—	—	l.f.	—	—	—	—	—	—	—	o.	—	—	—	—	—	r.	—	—	—	—	4	10
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	l.	—	1	2
o.	o.	o.	—	—	o.	o.	—	l.f.	o.	l.f.	—	f.	—	—	—	o., l.	o.	—	—	—	—	—	17	42
—	—	l.	—	—	o.	f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	12
o.	a.	o.	a.	f.	a.	o.	—	l.a.	l.a.	f.	f.	f.	f.	o.	o.	f.	f.	o.	o.	o.	—	o.	37	90
l.	o.	—	—	o.–f.	—	—	—	l.a.	o.	o.	o.	f.	—	—	—	f.	o.	—	—	—	—	—	13	32
o.–f.	—	—	—	—	—	o., l.	—	—	—	o.	—	—	—	—	—	—	—	—	—	f.	a.	—	5	12
o.	—	—	r.	—	—	—	—	—	o.	—	—	o.	—	o., l.	—	r.	—	o.	—	—	—	—	15	37
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	5
—	—	o.	—	—	—	—	—	r.	o.	o.	—	—	—	—	—	—	l.a.	—	—	—	—	o.	6	15
—	—	—	—	—	—	—	—	—	—	—	—	—	r.	—	—	—	—	o.	—	—	—	—	3	7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	r.–o.	—	—	—	—	—	—	—	—	4	10
r.	—	—	—	r.	—	—	—	r.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	17
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—	o.	o.	—	3	7
o.	a.	—	a.	a.	f.	o.	f.	l.	l.	f.	f.	l.	l.a.	f.	o.–f.	f.	l.a.	l.	v.a.	f.	a.	o.	40	98

Table I (*contd.*).

		Extreme W.		Western Downs (mainly wooded) (Cocking gap to River Arun)							West-central Downs (River Arun to River Adur)								
Aspect		E.	E.	N.N.W.	N.	W.	E.	S.	S.	N.	W.	W.N.W.	N.	N.	N.W.	N.	N.	N.	S.E.
Slope		24–35°	16°	18–20°	32°	10°	10–12°	22°					18–32°	22–32°	32–37°	15°	27°	27°	5°
	Life-form	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
Tragopogon minus	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.	—
Trifolium pratense	H	f.–l.a.	o.–f.	—	o.	o.	o.	o.	—	o.	o.	o.	o.	f.–a.	f.	f.	o.	o.	a.
T. procumbens	Th	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.
T. repens	H	—	o.–l.a.	—	—	o.	—	—	—	—	o.	o.	—	—	—	—	f.	—	o.
Trisetum flavescens	H	f.	—	o.	o.	f.	f.	—	—	f.	f.	o.	—	f.	a.	o.–f.	f.	f.	v.a.
Tussilago farfara	G	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Verbena officinalis	H	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Veronica chamaedrys	Ch	—	o.	—	o.	l.	o.	—	l.	—	—	—	—	o.	o.	o.	o.	—	l.
V. officinalis	Ch	—	—	—	—	—	—	—	—	—	—	—	—	—	—	f.	l.	—	r.
Vicia cracca	H	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	o.–f.	—
Viola hirta	H	l.	f.–l.a.	l.	—	—	l.	—	—	—	—	l.f.	—	o.	—	f.	l.f.	—	—
V. riviniana	H	—	o.	—	f.	—	—	—	—	—	—	—	—	—	—	o.	r.	—	—
Flowering plants 126																			
Bryophytes																			
Barbula cylindrica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Brachythecium purum	—	a.	a.	a.	f.	f.	l.a.	o.	f.	a.	f.	a.	a.	a.	f.	a.	a.	l.a.	—
Camptothecium lutescens	—	f.	a.	a.	o.	o.	—	—	v.a.	—	—	a.	f.	—	—	—	a.	—	v.a.
Dicranum scoparium	—	f.–a.	a.	l.a.	v.a.	—	—	o.	—	—	—	l.	—	f.	—	a.	a.	—	—
Fissidens adiantoides	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F. taxifolius	—	o.	—	—	—	o.	o.–f.	—	f.	o.	—	—	—	—	—	o.	o.	—	—
Hylocomium splendens	—	—	l.d.	—	v.a.	—	—	—	—	—	—	—	—	l.a.	l.a.	v.a.	v.a.	l.f.	—
H. squarrosum	—	o.	a.–l.d.	l.a.	f.–a.	o.	—	—	—	l.a.	o.	—	a.	o.	o.	l.f.	l.a.	—	a.
H. triquetrum	—	l.a.	a.	l.a.	a.	—	—	—	—	f.	—	l.f.	l.a.	a.	v.a.	l.a.	a.	l.a.	—
Hypnum chrysophyllum	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. cupressiforme *var.* elatum	—	o.	f.	l.	f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
H. cuspidatum	—	l.f.	o.	—	o.	f.	f.	—	—	—	—	—	l.a.	—	f.	o.	—	—	f.
H. molluscum	—	—	f.–a.	f.	o.–f.	—	—	—	—	—	—	—	—	—	—	—	f.	—	—
Mnium undulatum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Neckera crispa	—	—	o.–f.	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhacomitrium lanuginosum	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Seligeria calcarea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Thuidium abietinum	—	—	f.	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T. tamariscinum	—	—	o.	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Frullania tamarisci	—	—	o.–l.a.	—	l.a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scapania nemorosa	—	—	—	—	f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bryophytes 21																			
Lichens																			
Cladonia fimbriata	—	—	l.a.	—	l.a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. silvatica	—	l.f.	—	l.a.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Collema sp.	—	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Peltigera sp.	—	—	o.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lichens 4																			
Total species 151		74	68	50	52	64	56	38	29	36	41	45	45	44	46	51	58	39	58
Soils																			
Depth of sample		1–4″	—	0–2″	—	0–5″	—	—	—	0–2″	—	—	0–3″	—	0–2″	0–2″	0–2″	0–2″	—
Hydrogen-ion concentration (pH) ‖		7·4	—	7·4	—	6·9	—	—	—	7·2	—	—	7·8	—	7·6	7·2	6·9	6·5	—
Water loss at 100° C.		5·5	—	6·2	—	7·4	—	—	—	10·9	—	—	5·4	—	6·2	7·6	7·7	5·8	—
Loss on ignition (mainly organic matter)		20·5	—	25·9	—	32·0	—	—	—	38·2	—	—	17·3	—	28·2	30·6	31·6	24·0	—
CaO		17·4	—	27·4	—	11·1	—	—	—	2·4	—	—	33·7	—	30·2	1·9	21·7	25·7	—
Lime as $CaCO_3$		31·1	—	49·0	—	19·8	—	—	—	4·3	—	—	60·1	—	53·9	3·4	38·8	45·9	—
MgO		0·19	—	0·32	—	0·35	—	—	—	0·34	—	—	0·31	—	0·22	0·58	0·29	0·20	—
K_2O		0·21	—	0·58	—	0·29	—	—	—	0·36	—	—	0·26	—	0·17	0·34	0·31	0·16	—

‖ The pH determinations were made by the electrical method. 5 gr. soil were ground up and shaken with 50 c.c. $\frac{1}{5}$ saturated KCl and filtered.

Table I (*contd.*).

East-central Downs (River Adur to River Ouse)											Mount Caburn group east of Lewes				Eastern Downs: Firle region			Eastern Downs: Maritime region extreme east					Occurrences	
N. 15–25°	N. 30–32°	N. 30–35°	N. 32–37°	N. 37–40°	N. 22–24°	N.N.W. 30°	S.S.E. 30°	N. 35–37°	N. 30°	N. 30°	S. 23–28°	N. 23°	S. 18–32°	Flat	S. 10–15°	N. 30°	N. 30–32°	S.E. 20–24°	Flat	W. 5°	Flat	S.	No. of areas	%
19	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**		
r.	—	—	—	r.	—	—	—	—	r.	—	—	o.	—	—	—	—	—	—	—	—	—	—	5	12
f.	f.–a.	o.	a.	o.	o.	o.	—	o.	o.	o.	—	o.	—	o.	o.	o.	o.	f.	r.	o.	—	o.	36	87
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
o.	o.	—	o.	—	o.	—	—	—	—	—	—	—	—	o.	—	—	r.	—	—	o.	—	o.	14	35
f.	a.	—	a.	l.a.	a.	o.	—	f.	—	l.a.	—	o.	f.	—	—	f.	l.	f.	o.	—	—	—	28	70
—	—	—	—	l.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
l.	o.	—	—	—	f.	o.	—	o., l.a.	—	o.	—	f.–a.	—	—	—	—	l.f.	—	—	—	—	—	18	45
—	o.	—	—	—	—	o.	—	—	—	o.	—	r.	—	—	—	—	—	—	—	—	—	—	7	17
r.	—	—	—	—	r.	—	—	—	—	—	—	r.	—	—	—	—	—	—	—	—	—	—	4	10
o.	o.	—	—	o.	—	—	—	o.	o.	l.f.	—	—	o.	—	—	o.	l.f.	o.	r.	—	—	—	19	47
—	—	—	o.	o.–f.	o.	r.–o.	—	r.	o.	—	—	l.	—	—	—	—	—	—	—	—	—	—	11	27
—	—	—	—	—	—	—	No mosses	—	—	—	—	—	o.	No mosses	Mosses not noted	—	—	—	—	No mosses	No mosses	Mosses not noted	1	2
a.	a.	f.	l.a.	l.a.	f.–l.a.	f.		a.	a.	a.	f.	f.	f.–a.			v.a.	l.a.	f.	—				33	82
—	—	o.	f.	l.a.	—	—		—	—	—	—	—	f.–a.			f.	l.a.	—	l.				17	42
l.	l.a.	l.	—	l.	l.	l.f.		—	—	—	—	l.	—			l.a.	—	—	—				17	42
—	—	—	—	—	—	—		—	—	—	—	—	—			—	—	—	—				1	2
—	o.	—	—	—	—	o.		—	—	—	o.	—	l.f.			—	—	—	—				11	27
f.–l.a.	a.	—	—	l.a.	—	—		a.	f.–a.	a.	—	l.f.				a.	—	—	—				16	40
f.	f.	o.	—	o.	f.–l.a.	f.		a.	a.	a.	—	l.a.	—			f.	—	—	—				24	60
a.	v.a.	f.	a.	l.a.	v.a.	a.		—	l.a.	—	—	a.	—			v.a.	l.a.	—	—				23	56
—	—	—	—	—	—	—		—	—	—	—	—	—			—	—	—	—				1	2
—	—	—	—	l.	—	—		—	—	—	—	l.	—			—	—	—	—				6	15
o.	—	—	l.f.	—	l.f.	—		f.	—	f.	—	—	—			—	—	—	—				14	35
—	—	—	—	f.–l.a.	—	—		—	—	—	—	—	—			o.	—	—	—				6	15
—	—	—	—	—	—	—		o.	—	—	—	—	—			—	—	—	—				1	2
—	—	—	—	v.a.	—	—		—	—	—	o.	—	l.a.			l.a.	—	—	—				6	15
—	—	—	—	—	—	—		—	—	—	—	—	—			—	—	—	—				1	2
—	—	—	—	r.	—	—		—	—	—	—	—	—			—	—	—	—				1	2
—	—	—	—	—	—	—		—	—	—	—	—	—			—	—	—	—				2	5
—	—	—	—	—	—	—		—	—	—	—	—	—			—	—	—	—				2	5
—	—	—	—	l.a.	—	—		—	—	—	—	—	—			—	—	—	—				3	7
—	—	—	—	o.	—	—		—	—	—	—	—	—			—	—	—	—				2	5
—	—	—	—	—	—	—	—	—	—	—	o.	—	—	—	—	—	—	o.	—	—	—	—	4	10
—	—	—	—	—	—	—	—	—	—	—	—	—	l.a.	—	—	—	—	—	—	—	—	—	3	7
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2

19	19	20	21	22	23	24	25	26	27	28	29	29	30	30	31	32	33	34	35	36	37	38	39	40	41
65		48	40	44	56	58	37	26	48	42	53		34		58	46	34	26	57	59	50	24	29	23	31
	*					†					‡	§	‡	§											
0–3″	—	—	0–1″	0–3″	—		—	—	0–2″	—	0–4″	0–4″	0–2″	0–3″	—	—	0–4″	0–3″	0–4″	—	0–2″	—	0–4″	0–6″	0–4″
7·2	7·9	—	7·8	7·9	—	7·6	—	—	7·6	—	7·6	7·6	7·6	7·3	—	—	7·0	7·6	7·4	—	6·4	—	7·6	7·6	8·2
13·7	12·9	—	10·5	5·8	—	8·8	—	—	7·0	—	4·3	7·3	10·0	8·3	—	—	13·0	9·1	3·7	—	5·3	—	6·6	8·0	6·2
42·6	39·6	—	32·6	23·0	—	29·4	—	—	23·5	—	29·3	23·5	47·4	29·0	—	—	39·8	32·7	11·6	—	24·6	—	22·0	22·7	16·4
3·3	4·9	—	15·5	32·6	—	19·8	—	—	17·4	—	25·8	20·7	17·5	26·7	—	—	7·5	9·3	37·9	—	20·0	—	26·7	17·1	4·0
5·8	8·8	—	27·6	58·2	—	35·3	—	—	31·0	—	46·1	37·0	31·3	47·7	—	—	13·4	16·6	67·8	—	35·7	—	47·6	30·5	7·2
0·77	0·76	—	0·62	0·51	—	0·51	—	—	0·34	—	0·4	0·42	0·45	0·51	—	—	0·50	0·41	0·44	—	0·35	—	0·32	0·35	0·68
0·35	0·49	—	0·33	0·28	—	0·29	—	—	0·20	—	0·25	0·29	0·25	0·32	—	—	0·27	0·37	0·23	—	0·42	—	0·29	0·46	0·61

* Soil from mole heap dominated by *Festuca rubra* and *Thymus serpyllum*.

† Soil from mole heap with *Festuca rubra*.

‡ 1921.

§ 1923.

Table II.

	Chalk Heaths						Heaths	
	A	*B*	*C**	*D*	*E*	*F*	*a*	*b*
Achillea millefolium	f.	f.—a.	—	f.	a.	f.	f.	f.
Agrimonia eupatorium	—	—	l.	—	—	—	—	—
Agrostis alba	—	o.	a.	—	—	—	l.a.	f.
A. tenuis	f.	v.a.	l.a.	o.—v.a.	v.a.—d.	f.—l.a.	o.—f.	f.
Aira praecox	—	l.	—	—	—	—	—	—
Anthoxanthum odoratum	—	—	—	f.	l.a.	a.	o.	—
Anthyllis vulneraria	—	—	l.a.	o.	—	o.	—	—
Arenaria serpyllifolia	—	—	—	o.	o.	—	—	—
Asperula cynanchica	o.	o.	o.	a.	f.	o.	—	—
Avena pratensis	—	—	o.	f.	—	—	—	—
A. pubescens	—	l.a.	l.a.	—	—	—	—	—
Bellis perennis	o.	l.f.	o.	f.	f.	l.a.	—	—
Brachypodium pinnatum	—	—	l.d.	—	l.	l.d.	—	l.d.
B. silvaticum	—	l.	l.	—	—	—	l.	—
Briza media	o.	—	—	o.—f.	f.	f.	—	—
Bromus erectus	—	—	l.	—	—	—	—	—
B. mollis	—	—	l.	—	—	—	—	—
Calluna vulgaris	o.	f.	—	a.	o.—f.	f.	l.a.	l.a.
Campanula glomerata	—	—	—	—	—	—	o.	—
C. rotundifolia	f.	a.	—	f.	f.	—	f.	f.
Carex caryophyllea	a.	a.	—	f.	f.	o.	—	o.
C. flacca	a.	l.a.	—	f.	o.	o.—f.	l.a.	r.
C. pilulifera	—	—	—	—	—	—	l.a.	o.
Carlina vulgaris	—	—	o.	—	o.	o.	—	—
Centaurea nigra	—	—	r.	o.	—	—	—	o.
Cerastium vulgatum	—	—	—	o.	f.	—	—	—
Cirsium acaule	f.—a.	f.	o.	o.	f.	f.—a.	l.a.	—
C. arvense	—	—	o.	—	r.	—	o.	l.
C. lanceolatum	—	—	r.	—	r.	—	—	—
C. palustre	o.	o.	—	—	—	—	o.	o.
Clinopodium vulgare	—	—	—	—	—	—	r.	—
Crepis virens	—	o.	f.	—	—	—	—	—
Cynosurus cristatus	—	—	l.	f.	v.a.	o.	—	—
Dactylis glomerata	—	—	f.—a.	l.	—	f.	o.	—
Daucus carota	—	—	o.	r.	—	l.	—	—
Deschampsia caespitosa	—	—	—	—	l.	o.	—	—
Erica cinerea	—	—	—	—	—	o.	a.—d.	d.
Euphrasia nemorosa	o.	o.	o.	—	—	f.	o.	—
Festuca ovina	a.	v.a.—d.	a.	a.	v.a.	a.	a.	f.—l.a.
Filipendula hexapetala	—	—	—	a.	—	o.	—	l.
Fragaria vesca	l.	—	—	o.	—	—	l.f.	—
Galium mollugo	o.	—	—	—	—	—	—	—
G. saxatile	—	o.—f.	—	—	—	—	—	o.
G. verum	f.	o.—f.	l.	f.	—	o.	f.	—
Gentiana amarella	o.	—	—	o.	—	—	—	—
Helianthemum vulgare	—	—	—	—	—	—	l.	—
Hieracium pilosella	a.	f.	l.v.a.	f.	l.a.	—	l.	—
Hippocrepis comosa	—	—	—	f.	—	—	—	—
Holcus lanatus	l.	l.	l.	l.a.	l.v.a.	o.	l.f.	—
Hypericum perforatum	—	—	—	—	—	—	l.f.	—
H. pulchrum	—	—	—	—	—	—	o.	o.
Hypochaeris radicata	—	—	—	—	—	—	o.—f.	r.
Inula squarrosa	—	—	o.	—	—	—	o.	—
Koeleria gracilis	—	—	f.	f.	—	—	—	—
Leontodon autumnalis	f.	f.	o.	f.	o.	f.	o.	—
L. hispidus	f.	f.	o.	l.a.	—	—	o.	—
Linaria vulgaris	—	—	r.	—	—	—	—	—
Linum catharticum	f.	o.	a.	a.	o.	f.	—	—
Lotus corniculatus	a.	a.	a.	o.	a.	a.	a.	f.
Luzula campestris	o.	f.	—	—	o.	—	—	—
Medicago lupulina	—	—	a.	f.	—	o.	—	—
Origanum vulgare	—	—	l.	—	—	—	—	—
Phleum pratense	o.	—	l.	—	—	—	—	—
Phyteuma orbiculare	—	—	—	o.	—	o.—f.	—	—
Pimpinella saxifraga	—	—	o.	—	o.	o.	o.	o.
Plantago lanceolata	f.—a.	a.	a.	a.	a.	a.	f.	—

* This area is not a chalk heath but is situated on the plateau adjacent to chalk heaths and is included for comparison. Possibly it has been recently ploughed: see the soil analysis.

Table II (*contd.*).

	Chalk Heaths						Heaths	
	A	*B*	*C**	*D*	*E*	*F*	*a*	*b*
Plantago media	—	—	o.	—	—	—	—	—
Poa pratensis	—	—	l.a.	—	—	—	—	—
Polygala vulgaris	—	o.	—	f.	—	o.	—	—
Potentilla anserina	—	—	l.a.	—	—	—	—	—
P. erecta	o.	f.	—	o.	—	—	a.	—
P. reptans	r.	—	—	—	—	—	—	—
Poterium sanguisorba	l.f.	l.	l.f.	a.	f.—l.a.	a.	l.a.	l.a.
Prunella vulgaris	o.	o.	f.	o.—f.	f.	—	f.	—
Ranunculus bulbosus	—	—	f.	o.—f.	o.	o.	—	—
Rumex acetosa	r.	f.	—	—	f.	o.	o.	o.
Scabiosa arvensis	—	—	—	—	—	—	o.	—
S. columbaria	—	—	f.	o.	o.	o.	—	—
S. succisa	—	—	—	o.	—	—	l.a.	—
Senecio jacobaea	—	o.	—	—	o.	—	l.	o.
Sieglingia decumbens	—	—	—	l.a.	—	l.	—	o.
Silene cucubalus	—	—	o.	—	—	—	—	—
Stachys (Betonica) officinalis	—	—	—	—	—	—	l.a.	f
Taraxacum erythrospermum	—	—	—	o.	—	—	—	—
T. officinale	o.	o.	—	—	—	—	—	—
Teucrium scorodonia	—	—	—	—	—	—	l.a.	—
Thymus serpyllum	a.	f.	f.	f.—a.	a.	f.	f.—a.	l.
Trifolium pratense	—	o.	f.	f.	a.	o.	o.	—
T. procumbens	—	—	f.	—	—	—	—	—
T. repens	—	l.a.	o.	a.	v.a.	—	—	—
Trisetum flavescens	—	—	v.a.—d.	—	f.	o.	—	—
Ulex nanus (minor)	—	—	—	—	—	—	—	a.
Valeriana officinalis	—	r.	—	—	—	—	l.f.	—
Verbena officinalis	—	—	—	l.a.	—	—	—	—
Veronica chamaedrys	—	o.	—	o.	—	—	o.	—
V. officinalis	f.	o.	—	l.	—	—	o.	—
Viola hirta	—	—	—	l.	—	—	l.f.	—
V. riviniana	o.	l.a.	—	—	—	o.	f.	o.
MOSSES								
Barbula cylindrica	—	—	—	—	—	—	—	l.
Brachythecium purum	a.	a.	—	a.	a.	—	a.	a.
B. rutabulum	—	—	l.	—	—	—	—	—
Bryum capillare	—	—	—	—	l.	—	—	—
Camptothecium lutescens	l.a.	f.	—	—	v.a.	o.	—	—
Catharinea undulata	—	l.a.	—	—	—	—	—	—
Ceratodon purpureus	—	—	—	—	—	—	l.	—
Dicranum scoparium	v.a.	f.—a.	—	l.a.	l.	l.	f.	—
Hylocomium splendens	l.	—	—	—	—	—	—	—
H. squarrosum	f.	l.a.	—	—	f.	o.	—	l.
H. triquetrum	l.a.	l.a.	—	—	—	o.	—	—
Hypnum cupressiforme *var.* elatum	o.	—	—	—	—	—	—	—
H. cupressiforme *var.* ericetorum	—	l.a.	—	—	—	—	a.	l.a.
H. cuspidatum	—	o.	—	—	o.	o.	—	—
Polytrichum juniperinum	—	—	—	—	—	—	l.a.	—
Thuidium tamariscinum	—	—	—	—	—	—	f.	—
LICHENS								
Cladonia fimbriata	l.f.	l.	f.	—	—	f.	o.	—
C. silvatica	l.a.	—	—	—	—	—	f.	—
Cladonia sp.	l.a.	—	—	—	—	—	—	—
Peltigera sp.	—	—	—	—	—	—	o.	—
Total species 118	45	50	53	53	44	46	57	32

SOILS	A	B	C*	D	D	E	F	a	b
Depth of sample	0–4″	—	0–4″	0–2″	0–4″	—	0–6″	0–4″	0–8″
pH	6·9	—	7·4	6·0	6·5	—	6·9	5·8	4·6
Water loss of air dry soil at 100° C.	7·2	—	3·9	9·0	7·7	—	3·8	5·2	3·0
Loss on ignition (mainly organic)	26·8	—	16·1	41·7	24·9	—	17·7	19·5	12·6
CaO	0·97	—	6·6	2·0	1·2	—	0·53	0·62	0·51
As $CaCO_3$	1·74	—	10·0	3·6	2·1	—	0·95	1·11	0·92
MgO	0·21	—	0·60	0·62	0·47	—	0·28	0·38	0·39
K_2O	0·26	—	0·21	0·28	0·25	—	0·26	0·28	0·33

* This area is not a chalk heath but is situated on the plateau adjacent to chalk heaths and is included for comparison. Possibly it has been recently ploughed: see the soil analysis.

on gentle slopes and flat ground, and in the latter conditions become leached and tend to develop chalk heath.

It is noteworthy that the average pH value is nearly the same for all three types of soil, 7·4 to 7·5, though the range is fairly considerable (least in the dark humous soils).

Chalk Heath soils.

	CaO		Loss on ignition		pH	
	Average	Range	Average	Range	Average	Range
4 chalk heath soils	1·18	0·53–2·0	27·8	17·7–41·7	6·6	6·0–6·9

These soils are mostly brown with a relatively high humus content. They show a marked leaching of calcium and a range of pH values between 6 and 7.

Heath soils.

	CaO		Loss on ignition		pH	
	Average	Range	Average	Range	Average	Range
2 heath soils	0·56	0·51–0·62	16·05	12·6–19·5	5·2	4·6–5·8

The two soils examined from heath developed over the chalk were both light brown dry friable loams with a lower mean loss on ignition than the other soils. The average calcium content is lower than in the chalk heath soils and the pH value very markedly lower.

5. SOCIOLOGICAL CONSTITUTION OF CHALK GRASSLAND

In attempting to analyse the status and rôle of the 151 species listed in Table I we may take first the species which occur in 80 to 100 per cent. of the areas examined, i.e. those which possess the highest degree (5) of *constancy* in the terminology of the Zürich-Montpellier school[1], and next those with constancy 4 (60 to 80 per cent. of the areas)—Table III. These two categories contain the kernel of the association, though they do not exhaust the "characteristic" species, some of which are comparatively or even very rare.

The first column of figures gives the "percentage occurrence" of each species, i.e. the percentage of the whole number of areas listed in which it occurs, the second the "average abundance" of the species in the areas where it occurs. The "average abundance" figures have been arrived at by translating the frequency letters used in Table I into numbers, thus: v.a. or d. = 5, a. = 4, f. = 3, o. = 2, r. = 1: l. has been taken as 2, and where l. is prefixed to another symbol the next lower number is taken, thus l.a. = 3: where a range is indicated in the record the mean figure is taken, thus o.—f. = 2·5, o.—a. = 3. The sum of the numbers so obtained for each species is then divided by the number of areas in which the species occurs, and the number thus arrived at is entered to the nearest first decimal place for each species. It is doubtful if the very rough subjective estimates of abundance

[1] **Braun-Blanquet** and **Pavillard,** *Vocabulaire de Sociologie Végétale,* Montpellier, 1922 See notice in This JOURNAL, **10,** 1922, p. 245.

represented by the frequency letters can properly bear even this small amount of arithmetical treatment, but it is a great convenience to be able to use numbers, so the experiment has been made. It is clear that the treatment often masks some of the facts set out in Table I—not only the actual ranges of abundance, but also the special character of the mode of occurrence of certain species, e.g. *Bromus erectus*, which is nearly always recorded as generally "dominant," "locally dominant," or "local," whereas its "average abundance" arrived at by the plan described is 3, i.e. equivalent to "frequent." For indications of the actual modes of occurrence of the different species reference must be made to Table I. In the *Vocabulaire* provision is made for recording the kind of (static) distribution (Vertheilungsart) of the species and the extent of ground covered (Deckungsgrad, Arealprozent). These have not been studied in detail by any quantitative method, but the letter l. obviously refers to the former, and d. to the latter, though of course they are only qualitative characterisations. The figures in the third column ("exclusiveness") will be referred to later (p. 28).

Table III.

Species of constancy 5						Species of constancy 4				
Life-form	Species (16)	Per cent. occurrences	Average abundance	Exclusiveness		Life-form	Species (19)	Per cent. occurrences	Average abundance	Exclusiveness
G	Carex flacca	100	3·6	2		H	Achillea millefolium	76	2·8	2
H	Plantago lanceolata	100	3·3	2		H	Asperula cynanchica	76	2·9	4
H	Cirsium acaule	98	3·4	3		H	Hieracium pilosella	76	3·1	2
Ch	Thymus serpyllum	98	3·0	3		H	Plantago media	74	2·2	3
H	Avena pratensis	95	3·4	3		H	Dactylis glomerata	72	2·9	2
H	Briza media	95	2·9	3		H	Anthoxanthum odoratum	70	3·1	2
H	Festuca ovina	95	4·1	3		H	Phyteuma orbiculare	70	2·3	5
H	Poterium sanguisorba	95	3·9	4		H	Avena pubescens	70	3·2	3
Th	Linum catharticum	93	3·0	3		H	Trisetum flavescens	70	3·0	3
H	Lotus corniculatus	90	3·1	2		H	Campanula rotundifolia	67	2·7	2
H	Scabiosa columbaria	90	2·6	4		H	Centaurea nigra	67	2·4	2
H	Trifolium pratense	88	2·3	2		H	Bellis perennis	65	2·2	2
H	Koeleria gracilis	85	2·7	3		H	Galium verum	65	2·8	2
H	Pimpinella saxifraga	85	2·7	3		H	Prunella vulgaris	65	2·5	2
	Brachythecium purum	82	3·5	2		H	Ranunculus bulbosus	65	2·5	2
H	Leontodon hispidus	80	3·0	2		H	Bromus erectus	62	3·0	4
						Th	Euphrasia nemorosa	60	2·3	2
						H	Primula veris	60	2·0	3
							Hylocomium squarrosum	60	2·9	2
Average abundance of species of constancy 5			3·2			Average abundance of species of constancy 4			2·7	

It is noticeable that there is good correlation between the constancy and the average abundance (5 and 3·2, 4 and 2·7) of the species of greatest constancy included in these two lists, which means of course that the species occurring in most areas are also on the average most abundant in each area. The species of constancy 5 certainly form in most areas the bulk of the herbage: *Festuca ovina* in the first place, then, very commonly, *Poterium sanguisorba*,

which is often abundantly mixed in the turf throughout the sample. *Brachythecium purum* often forms an almost continuous lower layer, only appearing conspicuously on the surface when the turf is very short. Of the other dicotyledonous herbs *Lotus* and *Thymus* bulk largest of the most ubiquitous and abundant species, *Plantago lanceolata*, *Cirsium acaule* and *Leontodon hispidus* with their different habit of growth probably come next, with *Carex flacca*, and then the grasses *Avena pratensis* and *Briza media*. These are impressions, given in default of quantitative analyses of the herbage.

Of the species of constancy 4, *Galium verum* is important locally, sometimes almost rising to co-dominance. The grasses, both those which are specially characteristic of chalk (*Avena pubescens* and *Trisetum*) and those which are ubiquitous on most soils, like *Dactylis* and *Anthoxanthum*, are more local than those in the first list, but sometimes they rise to great abundance and even to dominance. *Bromus erectus* is in a special position. It is very local in the west of the region surveyed, being absent from the majority of the areas, but in the east it is frequently dominant over considerable areas.

Table IV.

Species of constancy 3					Species of constancy 2				
Life-form	Species (16)	Per cent. occurrences	Average abundance	Exclusiveness	Life-form	Species (19)	Per cent. occurrences	Average abundance	Exclusiveness
	Hylocomium triquetrum	56	3·7	2	H	Cynosurus cristatus	37	2·5	2
H	Agrostis alba	54	3·0	2	H	Daucus carota	37	2·3	3
H	Carlina vulgaris	54	2·0	3	H	Senecio jacobaea	37	1·7	2
H	Polygala vulgaris	54	2·1	2	H	Hippocrepis comosa	35	3·0	4
G	Carex caryophyllea	52	2·3	2	H	Trifolium repens	35	2·0	2
Th	Medicago lupulina	50	2·4	2		Hypnum cuspidatum	35	2·5	2
H	Holcus lanatus	47	2·3	2	H	Deschampsia caespitosa	32	2·6	2
H	Viola hirta	47	2·0	3	H	Phleum pratense	32	2·1	2
Ch	Cerastium vulgatum	45	2·0	2	H	Succisa pratensis	32	2·4	2
H	Galium erectum	45	2·2	3	H	Filipendula hexapetala	32	2·7	4
Ch	Veronica chamaedrys	45	2·2	2	H	Anthyllis vulneraria	30	2·4	4
H	Rumex acetosa	42	2·0	2	H	Leontodon autumnalis	30	2·3	2
	Camptothecium lutescens	42	3·3	3	G	Cirsium arvense	27	2·1	1
	Dicranum scoparium	42	2·9	2	H	Poa pratensis	27	2·3	2
Th	Gentiana amarella	40	2·0	3	H	Viola riviniana	27	1·6	2
	Hylocomium splendens	40	3·6	2		Fissidens taxifolius	27	2·1	2
					H	Arrhenatherum elatius	22	2·3	2
					H	Brachypodium pinnatum	20	2·5	4
					H	Festuca rubra	20	2·9	2
	Average abundance of species of constancy 3		2·5			Average abundance of species of constancy 2		2·3	

The species in Table IV again show a good correlation between constancy and average abundance (3 and 2·5, 2 and 2·3). It is noticeable that the only species of constancy 3 which exceed an average abundance of 3 are the three mosses *Hylocomium triquetrum* (a.a. 3·7), *H. splendens* (a.a. 3·6) and *Camptothecium lutescens* (a.a. 3·3). Of these the first two are abundant or very abundant

on steep northern exposures but not elsewhere. The last is locally very abundant on soils very chalky to the surface.

Hippocrepis comosa is the only species of constancy 2 which shows an average abundance of as much as 3. This is owing to its local abundance, rising to local dominance, forming large clans or societies, in many areas of the eastern half of the region. In the west it is only occasionally met with. *Festuca rubra*, occurring in only 20 per cent. of the areas examined, has an average abundance of 2·9. This again is owing to its local abundance, especially on loose friable soils showing a high pH value (see areas 24 and 41). *Filipendula hexapetala* (a.a. 2·7) also is locally abundant, especially in the east.

All these species, of relatively low constancy and relatively high frequency where they occur, are in one sense or another "characteristic" of the chalk grasslands of the Sussex Downs.

Table V. *Species* (81) *of constancy* 1; *i.e. occurring in less than* 20 *per cent. of the areas* (*arranged in order of average abundance*).

Life-form	Species	Per cent. occurrences	Average abundance	Exclusiveness
H	Agrostis tenuis	12	3·0	1
H	Festuca elatior	10	3·0	1
H	Potentilla reptans	2	3·0	1
	Hypnum molluscum	15	2·9	3
	Neckera crispa	15	2·9	3
	Frullania tamarisci	7	2·8	1
H	Senecio campestris	12	2·7	5
	Cladonia silvatica	7	2·7	2
Ch	Helianthemum vulgare	15	2·6	3
	Thuidium abietinum	5	2·5	3
	Scapania nemorosa	5	2·5	1
	Cladonia fimbriata	10	2·5	2
H	Ononis repens	17	2·4	2
	Hypnum cupressiforme *var.* elatum	15	2·3	3
H	Luzula campestris	15	2·2	2
H	Leucanthemum vulgare	17	2·1	2
H	Scabiosa arvensis	12	2·1	2
Th	Arenaria serpyllifolia	5	2·0	2
Th	Blackstonia perfoliata	2	2·0	2
Th	Bromus mollis	2	2·0	1
Ch	Calluna vulgaris	2	2·0	1
H	Campanula glomerata	12	2·0	4
H	Centaurea scabiosa	5	2·0	3
H	Cirsium palustre	5	2·0	2
Th	Crepis virens	10	2·0	2
H	Echium vulgare	2	2·0	1
G	Gymnadenia conopsea	7	2·0	3
H	Hypericum perforatum	10	2·0	2
H	Hypochaeris radicata	2	2·0	1
H	Lolium perenne	5	2·0	2
H	Origanum vulgare	15	2·0	3
H	Potentilla anserina	2	2·0	1
H	Potentilla erecta	7	2·0	1
Th.H	Reseda lutea	2	2·0	1
H	Sieglingia decumbens	5	2·0	1
Th	Sonchus oleraceus	15	2·0	1
G	Thesium linophyllum	7	2·0	5
Th	Trifolium procumbens	2	2·0	2
G	Tussilago farfara	2	2·0	1
H	Verbena officinalis	2	2·0	1
	Barbula cylindrica	2	2·0	1
	Fissidens adiantoides	2	2·0	1
	Hypnum chrysophyllum	2	2·0	3
	Mnium undulatum	2	2·0	1
	Rhacomitrium lanuginosum	2	2·0	1
	Thuidium tamariscinum	5	2·0	2
	Collema sp.	2	2·0	1
	Peltigera sp.	2	2·0	1
G	Ophrys apifera	15	1·9	4
H	Taraxacum erythrospermum	10	1·9	2
Ch	Veronica officinalis	17	1·9	1
H	Brachypodium silvaticum	12	1·8	1
Th	Myosotis arvensis	15	1·8	2
H	Arabis hirsuta	10	1·7	2
H	Clinopodium vulgare	7	1·7	2
H	Galium mollugo	7	1·7	1
G	Orchis maculata (type)	7	1·7	3
Th	Rhinathus crista-galli	10	1·7	2
H	Spiranthes autumnalis	7	1·7	2
H	Agrimonia eupatorium	7	1·5	2
Th	Bartsia odontites	5	1·5	1
H	Caucalis anthriscus	5	1·5	1
H	Cynoglossum officinale	5	1·5	1
Th	Erythraea centaurium	5	1·5	2
H	Fragaria vesca	5	1·5	1
Th.H	Linum angustifolium	2	1·5	2
G	Orchis pyramidalis	5	1·5	4
H	Ranunculus repens	5	1·5	1
H	Cirsium lanceolatum	17	1·4	2
H	Taraxacum officinale	17	1·4	1
H	Tragopogon minus	12	1·4	2
H	Vicia cracca	12	1·4	1
H	Picris hieracioides	10	1·2	2
G	Aceras anthropophora	2	1·0	5
H	Anthriscus silvestris	5	1·0	1
G	Habenaria viridis	2	1·0	2
H	Lathyrus pratensis	2	1·0	1
G	Listera ovata	5	1·0	2
H	Ranunculus acer	2	1·0	1
G	Tamus communis	2	1·0	1
	Seligeria calcarea	2	1·0	1

The species of constancy 1, i.e. those which occur in less than 20 per cent. of the areas listed, number no less than 81 species (64 flowering plants and 17 mosses, liverworts and lichens) or more than half the whole number. Many are casual invaders of the community; others are ubiquitous occasional constituents of grassland, but a few are confined to, or are mainly found in, chalk grassland or at least on soils rich in lime. In this last category we have the orchids *Aceras anthropophora* and *Ophrys apifera*, with *Gymnadenia conopsea*, *Orchis maculata* (type) and *O. pyramidalis*; *Blackstonia perfoliata* (also on clays), *Campanula glomerata*, *Centaurea scabiosa*, *Helianthemum vulgare*, *Reseda lutea*, *Senecio campestris*, *Thesium linophyllum*, and the mosses *Barbula cylindrica*, *Hypnum chrysophyllum*, *H. molluscum*, *Seligeria calcarea*.

Correlation of constancy and average abundance.

Species of constancy	Average abundance
5	3·2
4	2·7
3	2·5
2	2·3
1	1·9

The average abundance of all the species of constancy 1 is 1·9, of the flowering plants alone 1·8, of the bryophytes and lichens alone 2·2. Of the species of constancy 1 with relatively high average abundance we may note *Agrostis tenuis* (a.a. 3) which usually becomes abundant where it occurs on leached surface soils, *Festuca elatior* (a.a. 3), locally dominant on the deeper soils of steep northern slopes, *Potentilla reptans* (a.a. 3), locally abundant as an invader on open soil; *Senecio campestris* (a.a. 2·7), frequent or abundant in several eastern areas where it occurs, and *Helianthemum vulgare* (a.a. 2·6) locally abundant or even dominant here and there on short rabbit-eaten turf. While the first three are not constituents of most chalk grassland, the last two, though local, are very rarely found outside it, the former being of very restricted, the latter of wide distribution in Great Britain.

Exclusiveness. The figures in the last column of Tables III, IV and V constitute an attempt to represent by numbers the degree to which the species are exclusive to the association. According to the practice of the modern Swiss plant-sociologists[1], the figure 5 signifies "almost or quite confined to the association," 4 = "found especially in the association, though also (more rarely) in others," 3 = "preferring on the whole the community to others though also more or less abundant in these," 2 = "indifferent," 1 = "alien to the community."

It is evident that a just characterisation of the exclusiveness of a species in a given community can only be arrived at on the basis of an exhaustive

[1] **Braun-Blanquet** and **Pavillard**, *Vocabulaire*, p. 7; also other recent writings of the Zürich school (e.g. **Rübel** in This Journal, 8, p. 18).

knowledge of the constitution of the other communities in which it may occur, and such knowledge does not at present exist. Nevertheless it seems useful to make the attempt. One doubt which appears at the outset is the question whether the semi-natural grasslands of Great Britain developed on limestone formations (such as the carboniferous, oolitic and magnesian) other than the chalk should be reckoned with the chalk grasslands or not. They have so many species and other characters in common that this course might seem correct, but on the other hand a considerable number of the rarer characteristic chalk species are confined to the chalk itself, because the chalk is mainly a formation of the east and south-east of Great Britain, which is also a region of comparatively low rainfall, and thus the dry soil and calcicole continental species which just reach this country are often found upon it and do not extend beyond its area. The highest exclusiveness figure (5) has therefore been confined to those species which, so far as is known, never or very rarely occur in Great Britain except on the chalk.

Only 4 species, *Phyteuma orbiculare, Senecio campestris, Aceras anthropophora* and *Thesium linophyllum*, receive the highest figure 5[1]. It will be noted that while the first-named has a constancy coefficient of 4, occurring in 70 per cent. of the areas listed, the other three have a constancy figure of 1 only, having been met with respectively in 12 per cent., 2 per cent. (one occurrence) and 7 per cent. of the areas. *Phyteuma orbiculare* is confined to the chalk grassland of the southern counties, extending from Wiltshire and Dorset to East Kent, and the region dealt with in this paper coincides with that of its greatest frequency. *Senecio campestris* not only extends from Dorset to Kent, but also northward along the chalk outcrop to Lincolnshire. It is said to occur also in Gloucestershire and Northamptonshire (doubtless in oolitic grassland) and has been recorded also from Anglesea. Nevertheless its extreme rarity off the chalk warrants an exclusiveness figure of 5. The species is also decidedly local on the chalk through most of its range, and the eastern Sussex Downs, included in this survey, are probably the region of its greatest frequency. *Aceras anthropophora* is more eastern in its distribution than the other two species, its centre being Kent and Surrey, and though it is recorded from several places off the chalk[2], by far the greater number of plants undoubtedly occur in chalk grassland. *Thesium linophyllum* does not extend further north than Norfolk and except for two or three records in the west (Gloucester, Cornwall) it appears to be confined to chalk grassland.

If the whole area of the English chalk grasslands were surveyed there would, of course, be a number of other species not appearing in our survey records to which the exclusiveness figure 5 would belong. These would probably be most numerous on the chalk of Kent and Cambridgeshire.

[1] Whether a given species should receive an exclusiveness figure of 5 or 4 depends upon how the words "almost exclusively" are interpreted: *Aceras anthropophora* for instance might be thought to deserve 4 only.

[2] e.g. from sand hills in South Wales.

Of the eleven species receiving the exclusiveness figure 4, two have a constancy of 5, two of 4, four of 2, and three of 1.

Poterium sanguisorba is one of the most constant species of chalk and other limestone grassland from Perth and Forfar southwards, and is far more abundant and widespread on these than on any other soils. *Scabiosa columbaria*, while not so abundant, has a very similar distribution. It is perhaps a question whether these two should have 3 rather than 4 as an exclusiveness figure.

Asperula cynanchica has a much more limited distribution, not reaching Scotland, and is much more abundant in chalk grassland than anywhere else, though it occurs on other limestones. *Bromus erectus* has a more restricted distribution still and is a characteristic local chalk dominant, but it gets off the chalk sufficiently to have 4 rather than 5 as an exclusiveness figure.

Hippocrepis comosa is another species of southerly and easterly distribution scarcely reaching Scotland. It is locally very abundant in the chalk grassland. *Filipendula hexapetala* is of somewhat wider distribution but again is mainly concentrated on the chalk. *Anthyllis vulneraria* is much more widely spread in dry pastures than the preceding species but is much commoner on the chalk than elsewhere. *Brachypodium pinnatum* is of quite restricted southern and to some extent eastern and midland distribution. It occurs mainly on the chalk.

There are only three species of constancy 1 to which we have given the exclusiveness figure 4. *Campanula glomerata* is pretty widely distributed on dry pastures throughout Britain, but it is said to be rare in the west, and it is probably far more abundant on the chalk than elsewhere. *Ophrys apifera* has a more restricted distribution, scarcely reaching the extreme north of England and south Scotland. It is apparently strictly confined to limestone soils and by far the greater number of plants probably occur in chalk grassland, where, locally, and in certain years, it is extremely abundant. The distribution of *Orchis pyramidalis* is similar but it is not so strictly confined to limestone. Perhaps it should have an exclusiveness figure of 3 only.

Of the remaining species of constancy 1 a few are of some interest in relation to chalk grassland. *Lathyrus pratensis* was met with in one area and *Vicia cracca* in four established in the grassland. The latter, though its usual habitat is hedges and wood-edges may almost be considered an occasional constituent of chalk grassland. *Sonchus oleraceus* was met with in 5 areas as a colonist. *Tamus communis* is of course a wood-edge, and *Fragaria vesca* a woodland plant, the latter not very infrequently occurring in chalk grassland. *Tussilago farfara* is apparently a pioneer of loose chalk soils[1] which may remain for a time after a turf is established, though it does not flourish. *Cirsium palustre* (like *Agrostis alba* and *Carex flacca*) belongs to the numerous category of species that occur either on wet soils or on dry soils very rich in lime.

[1] See **Tansley** and **Adamson**. "The Chalk Grasslands of the Hampshire-Sussex border." This JOURNAL, **13**, pp. 180–183.

Twenty-eight species in all (eight out of the sixteen which have a constancy figure of 5) are marked as specially abundant in chalk grassland (excl. 3), sixty-nine species, or more than one-third of the whole list, as "indifferent" (excl. 2), and thirty-eight (none of which except *Cirsium arvense* rises above constancy 1) as "alien."

While there are thus large indifferent and alien elements (the latter due to the proximity of most of the Downs grassland to cultivated soil), comprising indeed more than two-thirds of the whole list of species, the association is, nevertheless, quite well characterised, according to the standards of the Swiss phytogeographers, by the 4 species of exclusiveness 5, the 11 of excl. 4 and the 28 of excl. 3, a total of 43 or 29 per cent. of the whole belonging to one of the three higher grades of exclusiveness. Of the 35 species of constancy 5 and 4, 17 or practically half belong to one of these three higher grades.

Life forms. Only 4 of Raunkiaer's life forms are represented in the list: chamaephytes, hemicryptophytes, geophytes and therophytes.

	Whole list of flowering plants		Species of constancy 5 and 4	
	No. of species	%	No. of species	%
Ch	6	5	1	3
H	91	72	29	88
G	13	10	1	3
Th	16	13	2	6

The preponderance of hemicryptophytes, very marked in the whole list of flowering plants, is even more overwhelming in the species of the two highest degrees of constancy which form the kernel of the vegetation. The other characteristic life form is the geophyte, to which nearly all the orchids belong, but which is not a type showing a high degree of constancy in this association.

It is hoped that this attempt to employ the methods of the Zürich school for the characterisation of this well-marked association and its species may have enabled a clearer picture to be formed of the floristic characters and composition of chalk grassland. It seems to us, however, that the ideal description and characterisation is only to be obtained by further study which will enable the species to be arranged in small, biologically homogeneous groups, rather of the nature of the *synusiae* of Gams[1], which can be characterised and classified in relation to (1) their ecological requirements, (2) the part they play in the economy of the association and its successional phases. By this means a much needed link may be found between the autecology of the species and the vegetational characters of the community.

6. STATUS OF CHALK GRASSLAND

It is obvious that the great bulk of the English chalk grassland is a community fixed and to some extent modified by continuous grazing. No special attention was paid to succession in the collection of the data for this paper,

[1] **Gams, H.** "Prinzipienfragen der Vegetationsforschung." *Vierteljahresschr. d. Naturf. Ges. in Zürich*, **63**, 1918.

the object being rather to collect floristic and soil data over a fairly wide region, but the observations made confirm and extend the conclusions arrived at in the third of these "Studies[1]." We may say with confidence that chalk grassland is a phase in the development of vegetation on a chalk soil, and that the mass of it is a biotically determined climax association, its characteristics being fixed by the continuous grazing factor. In Clements's terminology it is of course a *subclimax*—the true climatic climax being beechwood (*Fagetum silvaticae calcareum*[2], Beechwood on chalk[3], Beech consociation of sere 4[4]). With the biotic factor removed, or much diminished in intensity, two lines of development are indicated: (1) by leaching of the surface soil on flat surfaces or gentle slopes, a development to "chalk heath" and possibly heath, marked by the entrance and increasing dominance of *Calluna* and/or *Erica cinerea*, and their associates; (2) through a phase of scrub and ashwood to beechwood[5]. The first line may, however, be overtaken and obliterated by the second, though the details of this part of the development have not been studied.

In the grassland itself we may distinguish a consocies dominated by *Festuca ovina* or an associes in which this grass is very prominent, and it is this which forms the basis of the biotic subclimax. On the unleached soils, when grazing is relaxed, an associes dominated by meadow grasses is developed, and here heath development is excluded and the sere would doubtless progress to beechwood, though we are again ignorant of the details.

The cost of the soil analyses, which were carried out at the Cambridge University School of Agriculture, was defrayed by a grant from the Royal Society.

[1] **Tansley, A. G.** and **Adamson, R. S.** "The Chalk Grasslands of the Hampshire-Sussex Border." This JOURNAL, **13**, pp. 177–223.

[2] *Types of British Vegetation*, p. 163.

[3] **Adamson.** "The Woodlands of Ditcham Park." This JOURNAL, **9**, p. 120.

[4] **Watt.** "Development and Structure of Beech Communities on the Sussex Downs. Part II, Section III," "The Beech Consociation." This JOURNAL, **13**. See especially pp. 43, 63, 65, etc.

[5] **Tansley.** "Redevelopment of Woody Vegetation on Chalk Grassland." This JOURNAL, **10**, p. 168. **Watt,** *ibid.* Part II, Section I. "Preclimax Stages in the Developmental Succession." This JOURNAL, **12**, p. 145.

A SOIL SURVEY OF HINDHEAD COMMON[1]

By F. M. HAINES.

(*With sixteen Tables and three Figures in the Text.*)

CONTENTS.

INTRODUCTORY

The present communication deals with the results obtained from soil surveys carried out on Hindhead Common in July 1921, July 1922, and July 1923 together with a few further observations made in April and July 1924. A preliminary investigation on a relatively small number of samples was undertaken by Fritsch and Salisbury in 1914 (unpublished) with a view to elucidating some of the ecological problems of the heath, but since the results obtained shed little light upon the points at issue, it was suggested to the writer that a more general survey should be undertaken.

The area lies on the Hythe beds of the Lower Greensand, the subsoil being composed of stone and sand. The peat at different points is from 1 to 10 inches thick. Below this there are usually 4 to 6 inches of a light sandy soil, light both in texture and colour, overlying a hard sandstone which usually appears from 7 to 16 inches below the surface.

[1] From the Botanical Department, East London College.

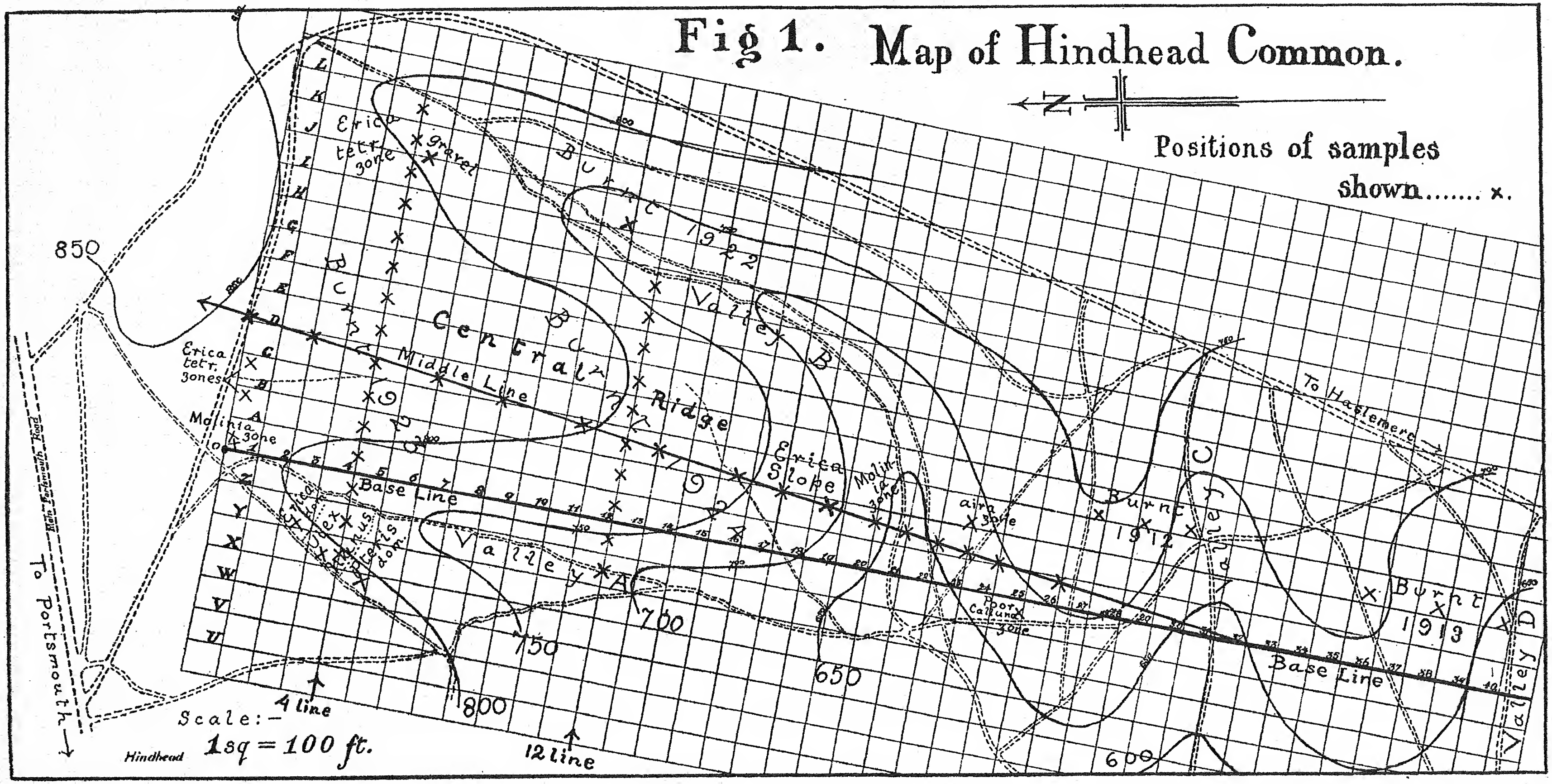
In July 1921 and July 1922 systematic surveys were made in which samples were taken at 100 feet intervals along three main transects across the area. Of these three lines two ran at right angles to the base line (cf. Fritsch and Parker (**9**)), one at the point 4 and one at the point 12, whilst the third or Middle Line ran along the summit of the central ridge as indicated in the accompanying map (Fig. 1). Samples were also taken from various zones of special interest such as areas recently burnt[1], the total number of samples taken amounting to about 270. In 1923 and 1924 the general survey was not repeated but a number of samples were taken from special zones and burnt areas. The analyses consisted in determinations of water content, hygroscopic moisture, humus, acidity, total salts, calcium and nitrates in samples from 2-inch and 9-inch depths at each point, but calcium and nitrates, though investigated throughout in the analyses of the first year, were not followed up in later years as the first year's results were all negative. In a few cases determinations were also made of aluminium and potassium.

PART I. METHODS

Method of sampling. All loose debris and undecomposed remains were first of all scraped from the surface. The upper inch of soil was then removed with a trowel over an area of about 20 square inches (6-inch circle), the soil of the next 2 inches was loosened and mixed and about 50 gm. were then removed and packed in lever-lid tins completely lined by a folding bag of two or three thicknesses of waxed paper. The tin containing the bag and soil was then weighed on the spot to 0·1 gm. on a balance capable of accuracy to 0·01 gm. if necessary. The amount of fresh soil taken was found on unpacking in the laboratory by difference after weighing the tins and packets. The samples were then air-dried in the laboratory until they attained a roughly constant weight which usually required from two to four months. For this purpose they were exposed in open paper trays lightly covered over with paper to prevent the access of dust. The water contents at this stage are recorded in the tables as hygroscopic moisture but are not always given. About 20 gm. from each sample were then placed in tared evaporating basins, weighed and dried to constant mass in an oven at 100–110° C. They were then re-weighed and the fresh and air-dry water contents calculated. For the determination of total salts and acidity extracts were then made by weighing out 5-gram lots (two from each sample) into 100 c.c. beakers and extracting by intermittent shaking for two hours with 20 c.c.

[1] Samples taken on lines were usually taken at points midway between the corners of the survey squares (see map) and are designated in the tables by the title of the line such as 4, 12, or ML (Middle Line) followed by the two numbers or letters between which they were taken. Thus 4 AB 2 signifies that the sample was taken on the 4 line between the points A and B, and at a 2-inch depth; ML 8, 9 and ML 18–19, 9 signify that the samples were taken on the Middle Line at the point 8, 9 inches deep and on the Middle Line between the points 18 and 19 and 9 inches deep respectively.

Fig 1. Map of Hindhead Common.



of conductivity water[1]. The cleanliness of the beakers was in all cases checked immediately before use by placing about 50 c.c. of conductivity water in the first of a row of two dozen or so (according to the size of the batch of samples), pouring it into each beaker in turn along the whole row and then ascertaining that its resistance in the conductivity pipette used was over 11,000 ohms. The process was always repeated until the resistance of the washing water that had been in all the beakers in turn became immeasurable on the bridge used (i.e. was over 11,000 ohms). After extraction the extracts were filtered through No. 40 Ashless Whatman filters which were shown to cause only a negligible increase in conductivity in their filtrates, the funnels for filtering being subjected before use to the same test as the beakers. The conductivities of the extracts were then found by means of the ordinary form of conductivity pipette used in conjunction with a bridge and telephone supplied by the Cambridge Scientific Instrument Company and reading direct by dial adjustments to the nearest 10 ohms. Accuracy to the nearest 10 ohms was found to be amply sufficient as it was always well within the ordinary error of sampling, individual 5-gram samples of the same soil often differing by 10–100 ohms, but in all cases the average was taken of the two readings for the two different extracts from the same sample, a third determination being made if necessary in cases of bad agreement. The values recorded in the tables for "Total salts" give the conductivities of the extracts in gemhos.

The acidities were determined electrometrically using a Clark hydrogen electrode, the extracts being run into the electrode vessel immediately from the conductivity pipette. The apparatus, which was capable with rapid working of accuracy to 0·001 volt (0·02 in the *p*H), was checked before and after every batch of extracts with standard solutions ($2N$ H_2SO_4 and $0{\cdot}1N$ alkali) so as to eliminate any possibility of error through changes in the condition of the electrode or formation of films on its surface or changes in the constants of the calomel electrode. In the 1922 survey (the first in which acidities were determined) a battery of voltameter cells with nickel electrodes and dilute NaOH as electrolyte was used as a source of hydrogen, the latter being subsequently passed over conc. H_2SO_4, through glass-wool filters, over an electrically heated coil of nichrome wire wound in a quartz tube and lastly over stick potash and a further glass-wool filter before entering the electrode vessel. In the later years, however, it was found that a Kipp's apparatus and potash tubes alone could be used as a source of hydrogen without any detriment to the accuracy of the results within the required limits, so this simpler form was substituted. The results with the two forms of generator were checked against one another and found to be identical within the required degree of accuracy and the apparatus has been checked against carefully prepared buffer solutions with the same result.

[1] Perfect wetting of the soil was ensured at the beginning of the extraction by grinding against the sides of the beaker with a thick hard glass rod.

The extracts normally took about five minutes to come to equilibrium, the equilibrium after such time being quite definite and steady, but frequently the time required was less.

In the 1921 and 1922 surveys the solutions were tested further for nitrates with diphenylamine and the residues left after filtering off the extracts were tested for calcium in a Collin's calcimeter. Both of these tests, however, were invariably negative so were not pursued in later years.

When the 5-gm. lots had been withdrawn from the dried sample and their extracts analysed as above, part or the whole of the remainder (about 10–20 gm.) was utilised for the determination of humus. For this purpose the soil was weighed in porcelain basins and heated to redness until further heating no longer produced any change in colour. Heating was discontinued when it became impossible to bring lighter layers to the surface on stirring, the process usually requiring from 4 to 6 hours, after which the basins plus ash were cooled and weighed.

In the determination of potassium and aluminium (when performed) extracts were prepared in conductivity water from the dry ground fine earth and subsequently filtered, added to the filter washings and concentrated. Potassium was estimated by the perchlorate method, being weighed as perchlorate on a Gooch crucible, and aluminium was estimated as Al_2O_3 by the ignition on foil of the hydroxide precipitated by NH_4OH. (Iron was first removed by precipitating $Fe(OH)_3$ and $Al(OH)_3$ together, taking up the filtered and washed precipitate in a minimum quantity of HCl, treating with NaOH, diluting, filtering and re-precipitating $Al(OH)_3$ alone from the filtrate with NH_4OH and NH_4Cl.)

PART II. RESULTS

THE GENERAL SURVEYS OF 1921 AND 1922.

Table I. *The* 4 *line in* 1921.

Soil	Water content		Humus		Total salts†		Coefficient of humidity		Salts/humus ratio	
	2″	9″	2″	9″	2″	9″	2″	9″	2″	9″
4 XY	1·2	4·4	17·3	1·2	4540	1099	0·07	3·67	262	915
4 YZ	3·0	3·2	10·3	1·6	2380	552	0·29	2·00	231	345
*4 Z 4	70·6	8·1	50·5	6·4	7410	2267	1·40	1·27	147	413
*4 4 A	78·3	2·1	10·8	1·2	2380	766	7·25	1·75	220	638
4 AB	6·2	1·6	9·9	1·0	2856	595	0·63	1·60	288	595
4 BC	18·9	2·0	28·3	0·9	4875	656	0·67	2·22	171	730
4 CD	3·9	2·0	15·4	2·3	4000	1738	0·25	0·87	260	755
4 DE	2·4	1·6	8·1	0·8	2220	837	0·30	2·00	274	105
4 EF	23·5	2·4	72·0	1·0	16670	1183	0·33	2·40	232	1183
4 FG	3·5	1·5	24·1	0·8	3450	800	0·15	1·88	143	1000
4 GH	3·0	2·6	15·1	1·7	3920	1015	0·20	1·53	260	596
4 HI	1·6	2·7	3·7	1·3	1695	953	0·43	2·08	458	732
4 IJ	4·9	9·2	1·7	1·6	1242	1439	2·88	5·75	730	900
4 JK	3·3	7·2	2·9	3·5	1449	1560	1·14	2·06	500	417
4 KL	11·8	11·2	13·2	11·7	3570	2500	0·89	0·96	270	214

* Samples marked with an * are treated as valley soils for the purpose of calculating the figures in Table VII: the remainder are soils more than half way up the hillsides and are called "tops."

† The total salts are expressed as the conductivity in gemhos of the extract made up as described on p. 34, see text.

Table II. *The 4 line in 1922.*

Soil	Water content		Humus		Total salts		Coefficient of humidity		Salts/humus ratio		pH	
	2″	9″	2″	9″	2″	9″	2″	9″	2″	9″	2″	9″
4 XY	12·9	8·5	6·7	2·2	2320	1430	1·90	3·86	346	650	3·6	3·8
4 YZ	15·4	7·8	5·6	1·8	2500	1148	2·75	4·33	446	638	3·4	3·8
*4 Z 4	59·6	17·7	31·8	2·3	7400	2468	1·87	7·70	233	107	3·2	3·5
*4 4 A	30·3	10·6	11·9	2·2	3920	1350	2·52	4·82	330	613	3·2	3·9
4 AB	13·5	6·8	5·6	0·6	2320	793	2·43	11·33	414	1320	3·1	3·6
4 BC	16·6	6·8	36·8	2·2	3030	1340	0·45	3·09	82	610	3·4	4·0
4 CD	20·7	—	8·9	2·9	3920	1072	2·32	—	440	370	3·2	3·6
4 DE	10·8	8·2	4·4	1·5	1722	1753	2·45	5·46	391	1170	3·8	3·5
4 EF	117·6	9·3	67·4	1·1	12980	1000	1·74	8·45	192	909	<2·8	4·1
4 FG	9·2	—	3·3	1·9	1438	1000	2·79	—	435	526	4·1	3·9
4 GH	10·5	9·6	1·6	1·4	1585	1110	6·56	6·86	990	792	3·9	3·9
4 HI	10·8	6·9	4·5	0·5	2350	627	2·40	13·80	522	1254	3·0	4·3
4 IJ	18·6	13·4	4·7	3·0	2896	2220	2·96	4·47	615	740	3·5	3·8
4 JK	13·4	15·2	14·9	2·6	2172	2172	0·90	5·80	155	835	3·9	4·2
4 KL	12·5	16·2	4·6	2·8	2102	2322	2·72	5·79	456	828	3·9	4·0

* See note to Table I.

Table II a. *Notes on vegetation in proximity of positions where soil samples were taken in 1921.*

4 XY (Recently burnt, 1920.) Dom. *Ulex nanus*. *Pteris* present. *Erica cinerea* small plants, 3 in. *Cuscuta* occasional on *Ulex nanus*. Few large clumps *Molinia* and numerous very small tufts. *Epilobium angustifolium* present but not frequent, 1½ ft. high, flowering. Peat, ¾ in. 2 in. dark soil. Sandstone 6–9 in. deep.

4 YZ (Recently burnt, 1920.) Dom. *Pteris*. *Ulex nanus* almost as abundant as *Pteris*. *Pteris* often 1–1½ ft. high. About one-third of the ground still bare. *Erica cinerea* almost all small plants about 9 in. or 1 ft. apart. *Cuscuta* occasional on *Ulex*. *Molinia* absent. Peat, ¾ in. 2 in. dark soil. Sandstone 1 ft. below surface.

4 Z 4 Dom. *Pteris*. *Vaccinium myrtillus* abundant, 1 ft. *Rubus* occasional bushes. *Ulex europaeus* to 30 ft. *Molinia* tufts fairly numerous. *Calluna* frequent. *Erica cinerea* less abundant. *Erica tetralix* present but not frequent. Dom. grass, *Nardus*. Dark soil 2½–3 in.

4 4 A Half way up slope. *Erica cinerea* and *Calluna* equally frequent. Average height of vegetation 1 ft. *Calluna* 2 ft. *Pteris* frequent, to 2½ ft.

4 AB Average *Calluna-Ulex-Erica*. *Betula* occasional. *Pinus* occasional. Average height of vegetation 10 in. *Calluna* 15 in. *Pteris* infrequent, to 1½ ft.

4 BC *Calluna-Ulex-Erica*. Less dense than at 4 AB, few bare patches. Average height of vegetation about 1 ft. *Calluna* rarely above 1 ft. except in hollows. *Pteris* infrequent, mainly about 1 ft., occasionally to 1½ ft. *Betula* and *Pinus* occasional. *Vaccinium myrtillus* occasional, to 5 in. Peat, 2½ in.

4 CD *Calluna-Ulex-Erica*. Number of bare patches. Average height of vegetation, 9–10 in. *Pteris* infrequent, mainly poor, about 1 ft. *Ulex nanus* 3 in. *Erica* 7–8 in. *Calluna* 9–10 in. *Betula* and *Pinus* absent.

4 DE As CD (above). *Pteris* nearly absent. *Pinus* occasional. *Cladonia* sp. frequent. Peat, 1 in.

4 EF Very thick vegetation, no bare patches. Dom. *Calluna*, to 2 ft. 6 in. *Erica cinerea* to 18 in. *Ulex nanus* less frequent than at DE and CD. *Festuca ovina* abundant. *Vaccinium myrtillus* very abundant, 8–9 in. high. *Pteris* frequent, to 2 ft. 6 in. *Pinus* occasional, to 5 ft. *Hypnum* sp. frequent. *Dicranum* on paths. *Usnea* sp. present, also *Parmelia physodes* frequent on dead *Calluna*. Peat, 4 in.

4 FG Vegetation sparse with bare patches. *Calluna-Ulex-Erica*. *Calluna* to 12 in. *Ulex* to 7 in. *Erica* to 8 in. *Ulex europaeus* occasional, 3–4 ft. *Pteris* sparse, 18 in. to 2 ft. *Vaccinium* to 4 in. *Rubus* occasional. *Festuca ovina* infrequent, also *Molinia* and *Deschampsia*. Peat, under 1 in.

4 GH *Calluna-Ulex-Erica* with bare patches. *Calluna* to 1 ft. *Ulex* to 4 in. *Erica cinerea* to 7–8 in. *Pteris* infrequent, to 1½ ft. Peat, ½ in.

4 HI As GH but more *Pteris*, to 18 in. Little *Molinia*. Generally vegetation very poor. Soil stony. No peat.

4 IJ Dom. *Calluna* to 3 ft. Vegetation very thick. *Erica* to 2 ft. No *Ulex*. *Molinia* tufts frequent. Small *Betula* occasional. No *Pteris*, except on sandy bare patches.

4 JK Vegetation tall, alternating with a number of bare patches. *Calluna* to 15 in. *Erica* equally frequent, 15 in. *Molinia* tufts frequent, 2–3 ft. *Pinus* occasional. *Betula* present. Very little humus.

4 KL Freshly burnt. Only *Molinia* sprouting.

Table III. *The 12 line in* 1921.

Soil	Water content 2″	Water content 9″	Humus 2″	Humus 9″	Total salts 2″	Total salts 9″	Coefficient of humidity 2″	Coefficient of humidity 9″	Salts/humus ratio 2″	Salts/humus ratio 9″
*12 YZ	15·0	6·2	19·1	1·4	5878	3120	0·78	4·43	308	223
*12 Z 12	16·5	2·2	29·5	2·2	6890	1562	0·56	1·00	234	710
12 12 A	21·5	7·2	8·4	3·5	9530	1923	2·56	2·06	1136	550
12 AB	12·1	2·0	32·8	1·4	6250	1150	0·37	1·43	191	821
12 BC	16·9	—	29·5	2·2	8330	1123	0·57	—	280	510
12 CD	53·5	2·1	12·6	1·0	4250	787	4·25	2·10	338	787
12 DE	2·8	3·2	2·7	0·6	1600	1515	1·03	5·33	592	2530
12 EF	0·4	2·8	16·2	3·0	3126	1905	0·03	0·93	193	635
12 FG	2·8	—	20·6	1·4	4000	763	0·14	—	194	545
12 GH	2·1	7·5	29·1	3·6	5550	1600	0·07	2·08	191	445

* Signifies considered as a valley soil for purposes of the calculation of the figures in Table VII.

Table IV. *The 12 line in* 1922.

Soil	Water content 2″	Water content 9″	Humus 2″	Humus 9″	Total salts 2″	Total salts 9″	Coefficient of humidity 2″	Coefficient of humidity 9″	Salts/humus ratio 2″	Salts/humus ratio 9″	pH 2″	pH 9″
*YZ	27·0	16·4	9·1	3·2	3445	1920	2·97	5·13	379	600	3·4	3·8
*Z 12	133·5	20·7	92·8	8·4	18150	4250	1·43	2·46	198	506	2·9	4·1
12 A	89·4	26·6	97·9	9·6	10000	4760	0·91	2·77	102	496	2·9	3·1
AB	41·7	—	36·4	—	6666	—	1·15	—	185	—	3·3	—
BC	64·7	8·3	22·0	1·0	5710	1000	2·94	8·30	260	1000	3·2	4·2
CD	26·3	4·6	12·4	1·4	4000	840	2·12	3·29	323	600	3·3	4·7
DE	7·1	21·8	2·6	7·7	1885	3030	2·74	2·84	725	394	3·9	3·2
EF	10·1	7·6	2·3	—	1428	733	4·40	—	620	—	3·8	4·3
FG	18·5	9·5	7·1	3·4	2752	1738	2·60	2·80	388	512	3·5	3·5
GH	41·7	9·5	17·8	2·3	6450	2630	2·34	4·14	362	115	2·9	3·8

* Samples marked with an * are treated as valley soils for the purpose of calculating the figures in Table VII: the remainder are treated as "tops." Cf. footnote to Table I, p. 37.

Table V. *The Middle Line in* 1921.

Soil	Water content 2″	Water content 9″	Humus 2″	Humus 9″	Total salts 2″	Total salts 9″	Coefficient of humidity 2″	Coefficient of humidity 9″	Salt/humus ratio 2″	Salt/humus ratio 9″
ML 0	9·3	11·4	17·7	7·5	4440	2150	0·53	1·52	251	287
ML 6	3·3	1·0	11·0	2·5	2856	631	0·30	0·40	260	252
ML 9	10·3	8·5	24·3	1·7	4540	757	0·42	5·00	187	445
ML 15–16	2·5	2·3	9·3	1·1	3278	1010	0·27	2·09	352	917
ML 17	7·0	1·1	11·0	0·7	2060	400	0·63	1·57	187	571
ML 18–19	2·1	0·9	9·1	1·1	2325	512	0·23	0·81	255	465
*ML 20	6·4	0·5	19·8	1·0	382	453	0·32	0·50	193	453
*ML 20–21	10·1	6·9	9·1	2·4	3918	1515	1·11	2·88	430	631
ML 23	5·4	10·2	10·8	2·0	2000	3030	0·50	5·10	185	1515
ML 26	2·5	2·1	6·3	1·3	1562	1103	0·40	1·62	248	848

* Samples marked with an * are treated as valley soils for the purpose of calculating the figures in Table VII: the remainder are treated as "tops." Cf. footnote to Table I, p. 37.

Table VI. *The Middle Line in* 1922.

Soil	Water content		Humus		Total salts		Coefficient of humidity		Salts/humus ratio		pH	
ML	2″	9″	2″	9″	2″	9″	2″	9″	2″	9″	2″	9″
0	40·5	23·3	13·6	7·5	5880	3840	2·98	3·11	433	512	3·3	3·7
2	13·8	29·8	3·6	5·7	1940	3330	3·84	5·23	539	594	3·7	4·3
6	10·6	10·6	4·1	1·7	2150	937	2·58	6·23	525	551	3·8	4·3
8	31·3	9·6	11·8	2·8	4340	2125	2·65	3·44	368	758	3·2	3·8
10–11	14·0	1·9	5·6	1·3	2665	800	2·50	1·46	475	615	3·0	4·2
13	9·8	11·3	3·7	3·8	1850	1650	2·65	2·98	500	435	3·7	4·0
15–16	21·9	—	16·0	1·3	5700	1098	1·37	—	356	844	3·1	3·4
17	11·2	5·9	5·1	2·5	2560	1050	2·20	2·36	502	420	3·2	3·8
18–19	27·7	9·3	25·2	3·1	5000	1885	1·10	3·00	198	608	3·3	3·3
*20	39·7	8·5	28·3	3·7	6250	1910	1·40	2·30	221	516	3·3	3·7
*21	92·1	25·6	5·1	4·3	4030	2500	18·10	5·95	790	581	3·8	4·1
22	29·5	102·9	10·1	2·4	3635	1480	2·92	42·90	360	617	3·4	3·3
23	—	8·2	—	6·1	—	1430	—	1·34	—	234	—	3·7
24	14·8	5·7	2·2	0·6	1784	533	6·73	9·50	810	888	3·4	4·0
26	34·8	34·3	16·3	1·9	4540	1665	2·13	18·04	278	876	3·5	4·0

* See note to Table I.

The results of the two general surveys are given in Tables I–VI and will serve to show the leading characteristics. The survey of 1921 was made after a very dry season and that of 1922 after a very wet one, so that differences in water content may be taken to represent practically the extreme conditions of the soil in this respect and must be realised to be due to the different seasonal conditions and not only to differences in the quantity or quality of the humus. The rainfall from Jan.–June recorded at Haslemere was 9·51 inches in 1921[1] and 21·19 inches in 1922[1] but it should be pointed out that in both years the samples were taken after a week of fine weather, so that excess of water content in the wet season is not attributable to rain immediately before sampling but represents as nearly as possible a fair equilibrium condition for a wet season. The samples in the two surveys were taken throughout (except where otherwise stated) at exactly the same points (within a few feet). Some notes are appended to the results of the 1921 survey in Table II a to show the condition of the vegetation at different points along one of the transects at the time of sampling.

In the case of the 4 line for which the notes are given the area from which the first two samples were taken had been recently burnt (about 1920) as indicated in the notes, the rest of the line running across heath about 5–6 years old, while of the 12 line with the exception of the first point, 12 YZ, the greater part lay on heath which was more than 15 years old. The rise and fall of the land along these lines can be realised from the contours on the map and also from Fig. 2, but the effect of varying height of slope and topographical position will be dealt with fully later.

The main characteristic of the soils in general, as will be seen at a glance from Tables II, IV and VI, is their very high degree of acidity, in view of which it is scarcely surprising that it was found to be impossible to demonstrate the presence of nitrates by means of diphenylamine and less still that

[1] Average for last 35 years, Jan. to June, 15·15 inches.

no calcium could be demonstrated with the Collin's calcimeter in any of the samples. No trace of nitrates could be detected in any of the extracts tested in the dilution stated although the reagent was shown to be sensitive to a solution of KNO_3 containing 1 part in 500,000[1]. That no nitrification took place in such acid soils was concluded as early as 1884 by Deherain (**7**) and in 1892 by Warrington (**27**), and Lipman and Wank (**20**) more recently, working on surface soils from the deltas of the San Joaquin and Sacramento rivers, found the peat of practically no value as a source of available nitrogen whether untreated or treated with steam and acid under pressure. Bryan (**3**) also finds that even the more resistant nitrogen bacteria such as those of the Soya bean are killed at an acidity of 3·5–3·9. On the other hand Fred and Davenport (**8**) find a critical *p*H of 3·3 for the Soya bean organism and a *p*H as low as 3·1 for that of *Lupinus* roots. Noyes and Conner (**22**) found that some nitrification took place in acid soils though the activity was increased by the addition of $CaCO_3$ and disappeared if the soil were left for a period fully saturated. Nitrification and nitrates have also been recorded in acid soils by Abbot, Conner and Smalley (**1**), Hall, Miller and Gimmingham (**11**), Houzeau (**13**), Petit (**23**), Temple (**26**), and White (**29**), but in the present cases only minute traces could be detected and it seems likely that the explanation lies in the high degree of acidity[2].

For calcium in one or two cases an alternative method was applied, the soil being treated with dilute HCl and the evolved CO_2 being carried by a stream of CO_2-free air drawn through the apparatus into standard alkali which was subsequently titrated against standard acid first with phenolphthalein and secondly with methyl orange. The method showed that even 10-gram samples contained no detectable quantity of calcium, the two titrations giving identical results. The calcium content of these soils is therefore extremely low throughout—a fact which accords well with what appears now to be generally accepted concerning the association of calcium deficiency and the characteristic symptoms of "sourness" which are exhibited by these soils. In the present case, however, it may be pointed out that the degree of acidity alone appears amply sufficient to explain these characters without calling in basic ratios to explain the facts.

The mean values of the *p*H values of the extracts containing 5 gm. soil to 20 c.c. water for all soils taken from areas of the average *Calluna-Ulex nanus-Erica* association were found to be 3·42 for the 2-inch depths and 3·9 for the 9-inch depths, the numbers being based on 38 and 39 samples respectively. The range of *p*H for 9-inch depths is from 4·7 to 3·1, but very few samples fall outside the range 4·3–3·5, only one sample having a *p*H

[1] The nitrate reaction could, however, just be detected in some of the soils with an extract of three times the stated strength, from which it appears that the nitrate content (as KNO_3) is of the order ·00027 per cent.

[2] The nature of some of the nitrogenous compounds which are present in peat is dealt with by **S. L. Jodidi** (**17**) and (**18**) and by **C. S. Robinson** (**24**).

above this upper limit and only a few isolated cases having a more acid lower limit than 3·5, this occurring where there happens to be more than 9 inches of peat. The range for 2-inch depths is from 3·9 to 2·3 but relatively few fall outside the range 3·0–3·6. Thus there is very considerable variation in the acidity even at fairly closely situated points, for which reason it was not considered necessary to record the acidities to more than one place of decimals. The 2-inch samples are almost invariably more acid than the corresponding 9-inch samples, as would be expected from their usually far greater content of organic matter, the 9-inch ones usually coming from a layer of light sandy soil immediately overlying the sandstone. Such a decrease in acidity in sandy soil below peat has also been found by Wherry (**28**) in the Middle Atlantic States and by Pierson Kelley (**19**) working on woodland soils from Chester County, Pennsylvania, who found an increase to 15 cm. below the surface and subsequently a decrease. The only exceptions to this rule of lower acidity at the 9-inch depths are found on bare, exposed gravel patches (cf. Fritsch and Parker (**9**)), which are still uncolonised and possess practically no humus (e.g. less than 1·5 per cent.).

In view of the fact that the acidities as determined by the electrical method and here recorded are of an exceptionally high order it appeared advisable to obtain additional confirmatory evidence of the presence of so large a quantity of acid by some alternative method. In some ten or so representative cases 10-gram lots of soil were accordingly weighed out, extracted with an excess of distilled water and the total titratable acids determined by titration of the extracts with phenolphthalein and $N/6{\cdot}5644$ NaOH. The results showed that the range of acidity in terms of normality of the ordinary 5 gm. : 20 c.c. extracts used would be from $N \times 0{\cdot}761 \times 10^{-3}$ in the case of a soil that had been burnt within the last few years to $N \times 9{\cdot}13 \times 10^{-3}$ in a *Molinia* zone rich in humus. In all the cases taken the acidity by titration was somewhat greater than that found electrometrically. This might be expected considering the probably very weak nature of the acids concerned. In one case in a soil from 3–4 XY the agreement was as close as 3·1 by electrometric determination and a normality of $N \times 1{\cdot}065 \times 10^{-3}$ by titration which (assuming complete dissociation) would correspond to a pH of 2·96, but in most cases the difference was greater.

The mean value as determined by titration on this relatively small number of samples is about $N \times 1{\cdot}49 \times 10^{-3}$ and it is interesting to note that the figure is of the same order as certain values recorded by H. Jeffreys (**15**) for "strongly acid" water from Wannister bog for which he gives the acidity determined by the same method as $N \times 13{\cdot}2 \times 10^{-4}$. The acidities are of a somewhat remarkable order, but when it is recalled that Olof Arrhenius (**2**) found that the rates of germination of ordinary crop plants such as barley, corn, cotton and wheat were only reduced respectively to about 1/2, 1/2, 1/3 and 1/6 of the normal rates in neutral solution when

grown on a soil made artificially so acid that an extract of 10 gm.: 50 c.c. water (approximately the same concentration as that used by the writer) showed a pH of 3, it becomes a little more believable that *Erica* and *Calluna* and their associates can permanently tolerate such hydrogen-ion concentrations as 2·3 as here seems to be the case, but fixation of nitrogen, which must be carried on by the fungal endophytes of these plants, does not appear yet to have been demonstrated in such circumstances. It has been noted by Healy and Karraker (**12**), however, also using the Clark hydrogen electrode, that air-dried soils showed a slightly greater acidity than fresh soil, so conditions in the field may not be so acute. On the other hand it has been stated by Conner (**6**) that moist soils show a loss in acidity on air drying.

Lastly a single acidity determination was made for the sake of additional evidence on an odd sample from near 3 Y by the sugar inversion method described in *Soil Science*, **15**, 2, by Parker and Bryan. The result showed an inversion of ·909 gm. sugar which, if one extrapolate a curve to their figures for more acid ranges, appears to correspond with a pH of about 3·5. A soil from this region in the previous year's survey gave 3·6 electrometrically.

Turning now to the question of the concentrations of total salts it will be seen that they average round a value of 4200 for the 2-inch depths and about 1200 for the 9-inch depths. These results are expressed as the conductivity in gemhos of the 5 gm. : 20 c.c. extracts in the particular conductivity pipette used. The pipette was standardised by finding in it the conductivity of a $N/100$ solution of KCl, such a solution having a resistance of 177 ohms and a conductivity therefore of 5650 gemhos. Thus the values given in the tables can be obtained in terms of $N/100$ KCl by dividing by 5650. An average sample of garden soil estimated in the same pipette showed a conductivity of 2600 gemhos so that it will be seen immediately by comparison that the heath soils can in no way be said to be particularly poor in their content of electrolytes but rather the reverse.

It will be seen from Tables I–VI and also from Fig. 2 that the total salts of the 2-inch depths, as likewise the water contents, run in general more or less parallel with the humus content. If the two sets of tables (i.e. I, III and V with II, IV and VI) be compared, however, apparent anomalies will be seen to occur where the alterations in total salts, etc. from one year to the next do not run parallel with those in humus as might be expected. Such is the case for instance in the first three points on the 4 line where the line runs down a recently burnt slope but these are special points which will be dealt with later under the effects of burning. In general the acidity, conductivity and water content run closely parallel with the humus content in the sense that would be expected. This is well illustrated in Fig. 2 which shows the variations in humus, water content, total salts and pH along the 4, 12 and Middle lines according to the 1922 survey. The thick lines at the base of the graphs

represent the rise and fall of the ground and their thicknesses represent the approximate heights of the vegetation at different points. Continuous lines all refer to 2-inch depths and dotted lines to 9-inch depths. In the lower graphs the thick lines (both continuous and dotted) give the percentages of humus and the thin lines water contents, in the upper the thick lines give the salt contents and the thin the acidities. The following general rules will be noticed: 2-inch humus contents run above 9-inch humus contents (i.e. thick continuous lines above thick dots in lower graphs); 2-inch water content is greater than 9-inch water content unless the humus percentages happen to be equal or the position is deep in a valley (e.g. in the bottom graphs the thin continuous lines run above the small dots except at 12 DE where the humus contents are equal and at ML 21–22 which is the bottom of a valley). Salt contents run parallel with humus (i.e. thick lines in the upper and lower graphs vary in the same sense) and vary more in the 2-inch depths than in the 9-inch. 2-inch acidities are nearly always greater than 9-inch acidities (thin continuous lines in the top graphs run above the small dotted lines) and 9-inch acidities usually vary in the same sense as the 2-inch. Acidities run parallel with humus contents, a real relation appearing to exist between them as found by Salisbury for woodlands (**25**), but have no fixed relation with water content, running parallel with water content when the percentage of humus is very large and in the opposite sense when the humus is low and the water content is nevertheless high through a low position on the slope.

The mean value of water soluble potassium in cases where it was determined was found to be 0·054 per cent. and of soluble aluminium 0·1148 per cent. of the dried fine earth.

The Effects of Wet and Dry Seasons.

The effects of wet and dry seasons as brought out by the 1921 and 1922 surveys are shown in Table VII which deals with the variations in water content and the distribution of soluble salts. Sections a–c of the table give the data for the individual lines, the numbers being averages of figures taken from Tables I–VI (see footnote to Table I), and section d shows means for all the tops and all the valleys taken together. It will be seen that in the individual cases the water content for the wet season (1922) may be as much as 600–700 per cent. greater than that for the dry season (Table VII c), the average increases, however, as shown by the figures in section e, being about two-and-a-half and three times the original percentage for 2-inch and 9-inch depths respectively. The coefficient of humidity in the individual cases increases from three to seven times and in the aggregate (section e) becomes about three times the original value, i.e. increases by about 190 per cent. in both depths. It will be seen that the greatest variation in *actual* water contents (VII d) is found in the 9-inch depths on high ground, the next greatest in 2-inch depths on high ground to which the 9-inch valleys

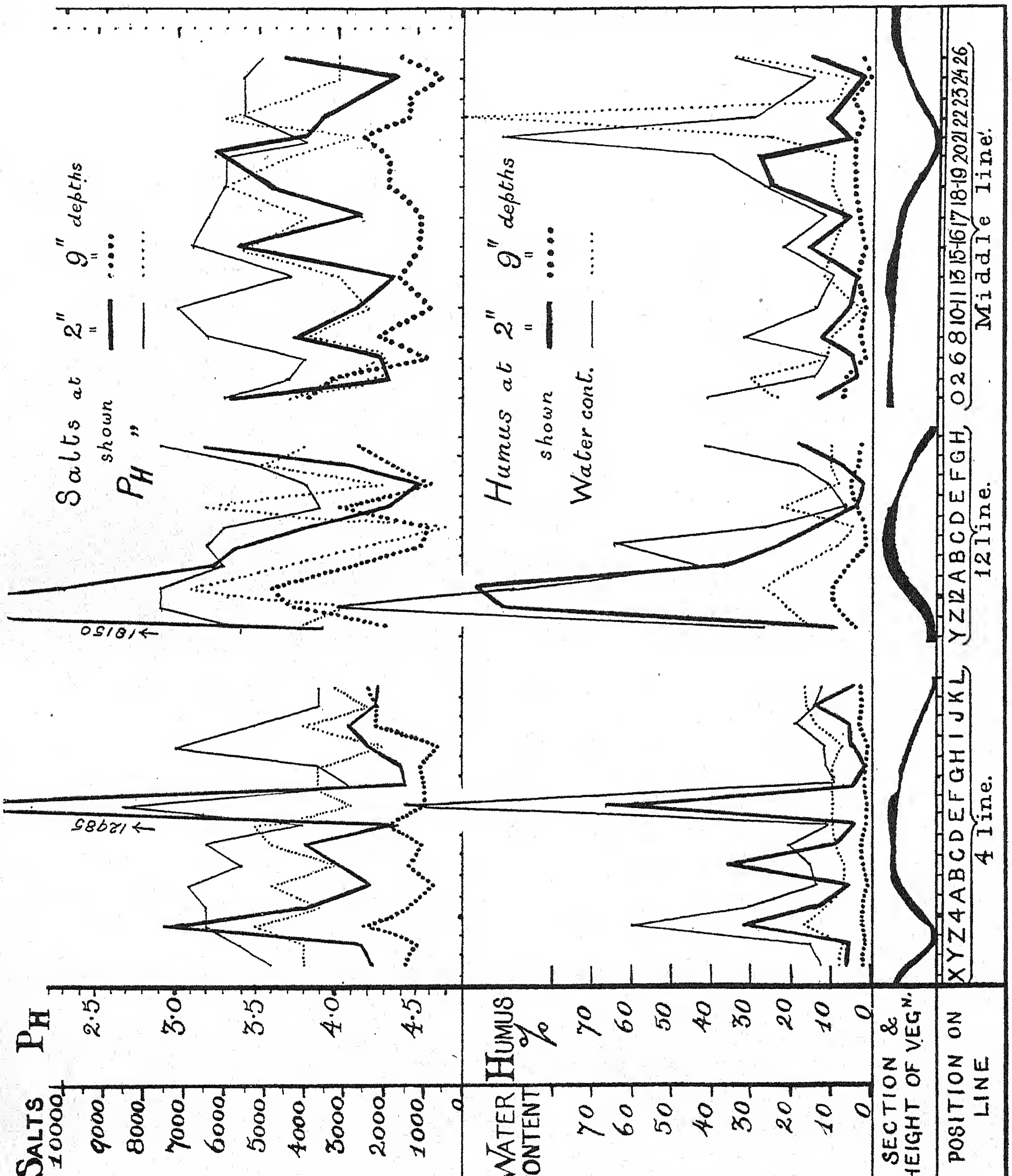


FIG. 2. Curves showing variations in humus, water content, total salts and acidity along three main transects across the area in 1922. For positions of points see Map (Fig. 1). For full explanation see text, pp. 43–44.

run very close and the least variation in the 2-inch depths in the valleys. These points, however, as seen in section d of Table VII, do not probably present the matter quite in its true light, as part of the 4 line which has been included in calculating these means had been burnt only about a year previously to taking the 1921 observations. The values for the water contents and the coefficients of humidity therefore become anomalously high in the valleys in the first (dry) season through the increased facility of drainage down the slopes. The effect of including the values for the 4 line is thus erroneously to reduce the apparent percentage increases in these values from 1921 to 1922 by making the means for 1921 appear much too high. Probably the correct impression is that given in Tables VII d′ and e′, where the values have been calculated neglecting the anomalous 4 line. From these values it will be seen that the greatest variation in actual water content is really in the 2-inch depths in the valleys, the next greatest in 9-inch depths in the valleys, next in 9-inch tops and least in the 2-inch tops though even here it is increased by 188 per cent. or to nearly three times. The general increase is to about three-and-a-half times in both 2-inch and 9-inch depths but the valleys experience both a higher water content and a greater range in water content than the "tops." (See footnote to Table I, p. 37.)

Probably of greater importance are the variations in water content compared with the amount of humus, or the variations in the coefficient of humidity. These are also recorded in section d and their corrected values ignoring the 4 line in section d′. It will be seen that the humidity is frequently greater on the tops of the slopes than in the valleys, especially in the 9-inch depths in a wet season where it seems to be universally so (VII a, b, c), and in 2-inch depths in both seasons in the case of the very old heath on the 12 line. Otherwise the coefficient of humidity for 2-inch depths is distinctly greater in the valleys (VII a and c), the valleys also experiencing far greater fluctuation in humidity in the different seasons as far as their 2-inch depths are concerned (VII d′), the 9-inch depths fluctuating very much less than the 2-inch and by almost exactly the same amount on the tops and in the valleys. The changes in the coefficient of humidity or "effective wetness" of the soil run closely parallel with those in actual water content in the case of the 2-inch depths but appear to show a less marked relation in the 9-inch depths, a large increase in water content leading here to a relatively small one in the coefficient of humidity (VII d′), especially in the valleys. This result might be expected since in the 2-inch depths the humus must be responsible for holding practically the whole of the water, while in the 9-inch depths where most of the water would, owing to the relative paucity in humus, be held by the sandy mineral fractions of the soil any increase in the amount of humus (as has here taken place) would naturally considerably depress the coefficient. Where the water is originally held mainly by the sand the action of added humus might be compared with

that of a sponge, reducing the "wetness" produced by a given water content, so that the relatively low increase in the 9-inch depth coefficient (80 per cent.) is evidently explained by the incident that a particularly large increase in the percentage of humus happened to take place at this depth during this year, as shown in the last column of section d′ of the table.

Table VII. *Mean Values of the water content, humus content, coefficient of humidity, and total salts compared for high- and low-lying ground in dry and wet seasons* (1921 *and* 1922).

	Position of samples and year	Water content 2″	Water content 9″	Humus 2″	Humus 9″	Coefficient of humidity 2″	Coefficient of humidity 9″	Total salts 2″	Total salts 9″
a	4 line, tops, 1921	5·3	3·6	17·4	1·5	0·6	2·3	2988	1027
	1922	22·5	9·3	13·7	1·8	2·5	6·7	3267	1305
	4 line, valleys, 1921	53·6	6·3	24·8	6·2	3·2	1·3	4440	1978
	1922	34·1	14·5	16·1	2·4	2·5	4·7	4474	2047
b	12 line, tops, 1921	14·0	12·5	15·2	2·1	1·1	2·3	5330	1346
	1922	37·4	12·6	24·8	4·2	2·4	4·0	4858	2103
	12 line, valleys, 1921	14·7	4·2	24·3	1·8	0·7	2·7	6384	2341
	1922	80·2	18·5	50·9	5·8	2·2	3·8	10777	3085
c	ML, tops, 1921	5·3	4·8	12·4	2·3	0·4	2·1	2883	1199
	1922	22·4	25·2	7·9	3·1	2·8	8·1	3508	2232
	ML, valleys, 1921	8·2	3·7	14·4	1·7	0·6	2·2	1432	1432
	1922	60·9	17·1	16·7	4·0	3·6	4·3	5140	2205
d	*Mean values:*								
	All tops, 1921	8·2	4·3	16·5	1·8	0·70	2·31	4100	1174
	1922	25·9	14·9	15·0	2·8	2·60	6·80	3755	2270
	Valleys, 1921	29·8	5·3	21·7	3·8	1·76	1·83	4350	1790
	1922	56·4	16·5	26·2	3·8	4·43	4·88	6470	2390
	Increase shown by tops:	216 %	247 %	−9·0 %	55 %	271 %	194 %	−8·3 %	+93 %
	Increase shown by valleys:	89 %	212 %	21 %	0·0 %	152 %	167 %	49 %	34 %
e	General increase on basis of all samples taken:	151 %	199 %	3·5 %	48 %	195 %	190 %	2·5 %	77 %

Table VII. *Sections d′ and e′.*

(The Table gives the mean values for the water contents and coefficients of humidity for high and low ground in dry and wet seasons calculated as in Table VII, sections d and e, but ignoring the 4 line which is anomalous through having been in part recently burnt.)

	Position of samples and year	Water content 2″	Water content 9″	Coefficient of humidity 2″	Coefficient of humidity 9″	Humus 2″	Humus 9″
d′	All tops, 1921	9·7	5·2	0·77	2·29	15·8	2·2
	1922	27·9	17·9	2·65	6·86	15·8	3·5
	Valleys, 1921	12·0	4·0	0·69	2·20	19·4	1·75
	1922	73·1	17·8	5·72	3·96	33·6	4·9
	Increase shown by tops	188 %	244 %	242 %	200 %	0·0 %	59 %
	Increase shown by valleys	510 %	345 %	758 %	80 %	73 %	180 %
e′	General increase on basis of all samples taken except the 4 line:	247 %	265 %	325 %	179 %	14 %	81 %

Concerning the effects of a wet season on the redistribution of soluble salts it would appear from a superficial glance at the figures in the last columns of Table VII d that the effect has been to cause a considerable increase in the conductivity of the 9-inch depths (93 per cent.) on the tops at the expense of the 2-inch depths and an all round increase in the valleys. The appearance happens to be roughly correct in so far as the valleys are concerned but is misleading for the tops, since in taking the changes in the amounts of soluble salts as an indication of the leaching effects it is evidently not sufficient to take only the actual salt concentrations into account but the salt concentrations compared with the percentage of humus. If the amount of humus present be also taken into account it is found that there is a general loss by both depths at the tops and a general gain by both depths in the valleys, the 2-inch depths in both cases changing by the greater amount. Thus the lower layers (9-inch) on the tops do not gain in salts by leaching from the upper layers as appears from Table VII d, but the apparently greater quantities of soluble salts in the 9-inch depths are only due not to leaching but to an incidental increase in the percentage of humus. The true effects of leaching during the wet season may be gathered from Table VII f in which the ratios of total salts/humus are compared for the different layers in the two seasons. The changes in this ratio are taken to be a fairer indication of the leaching or drainage effects than those in actual conductivity, since changes in the latter are not only due to leaching but also to variations in the amount of humus present.

It is taken, moreover, that a measure of the effect of leaching or drainage on any part of a slope is given by the difference between the change in salts/humus ratio for the relevant part of the slope and the aggregate change for the whole slope. Thus supposing that there were found to be in one year an aggregate increase in the amount of salts per unit amount of humus of 1 per cent. it is taken that if no leaching or drainage occurred the salts/humus ratio at all points on the slope would show an approximately uniform increase of 1 per cent. If now leaching or drainage cause a redistribution of the salts the ratio will decrease in some places and increase in others. If in some particular region the ratio were found to have increased by 5 per cent. the drainage or leaching effect would be taken to be proportional to 4, since there would have been an increase of 1 per cent. without any leaching and the leaching has accounted for an additional change of 4 per cent. If in another part there were no change in the ratio leaching would have accounted for a loss of the 1 per cent. that would have been normally gained if no leaching had occurred. The leaching effect on any soil given in Table VII f therefore is the difference between the percentage change in the ratio of salts/humus for the relevant part of the slope and the aggregate percentage change in the ratio for the whole slope.

Table VII f. *Changes in the salts/humus ratio and the effect of leaching and drainage from* 1921 *to* 1922.

Soil samples from which the results are calculated	Year	Mean values of ratio of total salts/humus			
		2″		9″	
Means based on all samples taken from the 4-, 12- and middle lines (35 samples in 1921 and 40 in 1922 from each depth)	1921 1922	308 427		690 648	
Increase	—	—	38 %	—	−6 %
All tops	1921 1922	326 439		730 674	
Increase	—	—	34·5 %	—	−7·7 %
Leaching effect	—	—	3·5 % loss	—	1·7 % loss
All valleys	1921 1922	224 372		511 536	
Increase	—	—	66 %	—	5 %
Leaching effect	—	—	27·2 % gain	—	11 % gain

It will be seen from the table (VII f) that the leaching effect on 2-inch depths on high ground has been to cause a loss of 3·5 per cent. since there has only been a gain of 34·5 per cent. instead of 38 per cent., and the effect on 9-inch depths on high ground has been to cause a loss of 1·7 per cent. as the decrease is 7·7 per cent. instead of only 6 per cent. and so on. The means[1] at the beginning of the table show that there has been a general increase in total salts during the year's interval of 38 per cent. in the 2-inch depths and a slight decrease (6 per cent.) in the 9-inch. In the aggregate then there is no gain in salts by loss through leaching from the upper layers. If leaching due to greater rainfall played a part in increasing the salts at 9-inch depths at the expense of the supply in the 2-inch depths a greater increase in the concentration of salts per given amount of humus should be found in the 9-inch layers after a wet season than in the 2-inch layers but actually on the tops the proportion of salts to humus in the 9-inch layers has decreased and in the valleys has only increased to less than half the extent shown by the 2-inch depths. It is to be concluded that there is a general loss on the tops, the 9-inch layers losing more by drainage than they receive by leaching, and a large increase in the valleys which is much more pronounced in the 2-inch depths than in the 9-inch.

Table VII g. *Ratios of* $\dfrac{\textit{salts/humus for wet season}}{\textit{salts/humus for dry season}}$.

Mean values:

2″ tops	1·345	All tops	1·05
9″ tops	0·923	All valleys	1·24
2″ valleys	1·660	All 2″ depths	1·61
9″ valleys	1·050	All 9″ depths	0·974

[1] Founded on 37 samples in each year from each depth.

Table VII h. *Salts/humus ratio for the* 12 *line slope in* 1921 *and* 1922.

		Salts 2″	Humus 2″	Salts/humus ratio 2″
Top, 12 AB	1921	6250	32·7	191
	1922	6666	36·4	183
Bottom, 12 12 Z	1921	6890	29·4	234
	1922	18150	92·8	195

That the wet season does not cause the 9-inch layers to gain appreciably at the expense of the 2-inch is also seen from the figures in Table VII g which not only bring out the greater increase on the low-lying ground at the expense of the high in a wet season but also show that the salts/humus ratio has increased in the aggregate to 1·61 times its original value in all the 2-inch depths taken together and has decreased slightly, to ·97 of its original value, in the aggregate 9-inch depths.

The effects of leaching on burnt ground will be dealt with below.

The Effects of Fires.

The effects of fires on the soil are shown in Table VIII, the first part of the table giving the results in individual cases as shown by comparing the properties immediately before and immediately after the fires and the last part of the table giving the aggregate results as shown by means.

It will be noticed (cf. Fritsch and Salisbury (**10**)) that on the average a fire leads to the destruction of 60 per cent. of the original humus in the surface soil (leaving, e.g., 8·6 per cent. instead of 20·9 per cent.) and only about 8 per cent. of that lower down at the 9-inch level. The effects, however, are distinctly different according to the age and height of the vegetation that is burnt and the consequent actual total amount of humus originally present in the soil. In relatively young heaths, burning, it will be seen, leads to the destruction of 66 per cent. of the original organic matter in the 2-inch depths, but in the case of very old heath, bearing *Calluna* to a height of 3–4 feet and with a very high original percentage of humus, as much as 70 per cent. of the original humus may remain after firing. In consequence of the destruction of the humus the water content of the 2-inch layers falls on the average to about one-third of its original value, but that of the deeper layers is practically unaffected or may slightly increase through the more ready percolation (see page 59) from the upper layers.

Concerning the effects on the concentrations of soluble salts, it is to be supposed (see below) that the immediate effect is always to increase the total salts though this can only be demonstrated in soils where a large amount of humus is left after burning and the analysis can be made at a very short interval after the fire. It is only shown in Table VIII in the case of 12 AB, the only one where these conditions were obtained, but is probably a general feature and due to the liberation of salts from the burnt plant remains.

A few months after the fire, as shown by the means at the bottom of the table, the general effect is a decrease in total salts both in the 2-inch and 9-inch depths. The resulting reduced concentration of salts is on the aggregate about 70 per cent. of the original concentration in 2-inch depths and 86 per cent. of the original in 9-inch depths. The results are explained by the more ready leaching after the destruction of the humus (see p. 59) and naturally the effect is, as shown by the table, greater in the surface than in the lower layers. Burning then leads to a serious loss of salts, since the leaching effects when the humus is destroyed more than balance the gains of salts from the plant remains.

Table VIII. *Effect of burning.*

	Soil sample	Burnt in		Water content 2″	Water content 9″	Humus 2″	Humus 9″	Total salts 2″	Total salts 9″	Coefficient of humidity 2″	Coefficient of humidity 9″	Salts/humus ratio 2″	Salts/humus ratio 9″	pH 2″	pH 9″
Young heaths	4 4 A	1923	before	30·3	10·6	11·9	2·2	3920	1350	2·54	4·81	328	613	3·2	3·9
	,,	,,	after	9·6	7·8	8·5	2·3	2700	1105	1·13	3·39	318	480	3·3	3·2
	4 AB	1923	before	13·5	6·8	5·6	0·6	2320	793	2·41	11·42	415	1320	3·1	3·6
	,,	,,	after	8·2	—	4·9	—	1598	—	1·67	—	326	—	3·4	—
	4 BC	1923	before	7·2	5·6	36·8	2·2	3030	1340	0·20	2·55	82	609	3·4	4·0
	,,	,,	after	6·2	—	1·3	—	914	—	4·70	—	704	—	3·5	—
	15 D	1924	before	—	—	7·6	—	1520	—	—	—	200	—	3·6	—
	,,	,,	after	—	—	6·0	1·5	1197	624	—	—	199	416	3·8	4·1
	4 A–C aver.	1923	before	17·0	7·7	18·1	1·7	3090	1161	1·38	6·26	275	847	3·2	3·8
			after	8·0	7·8	4·9	2·3	1737	1105	2·50	3·39	449	480	3·4	3·2
Old heaths	12 AB	1924	before	41·7	1·7	36·4	13·3	6666	602	1·15	0·13	184	45	3·3	4·0
	,,	,,	after	—	—	—	—	7140	—	—	—	—	—	3·3	—
	12 12 A	1924	before	31·5	—	27·3	—	5780	—	1·15	—	212	—	2·7	—
	12 B	,,	after	—	—	22·4	—	2435	—	—	—	109	—	3·5	—
Mean values for oldest heath			before	36·6	1·7	31·8	13·3	6223	602	1·15	0·13	198	45	3·0	4·0
			after	—	—	22·4	—	4787	—	—	—	109	—	3·4	—
Means for younger heath			before	17·0	7·7	15·5	1·7	2698	1161	1·72	6·26	256	848	3·3	3·8
			after	8·0	7·8	5·2	1·9	1602	864	2·50	3·39	387	448	3·5	3·6
Means of all values together			before	24·8	6·18	20·93	2·07	3872	1021	1·49	4·73	232	647	3·2	3·88
			after	8·0	7·80	8·58	1·90	2664	864	2·50	3·39	331	448	3·5	3·65

Repeated burning would therefore lead to a steady impoverishment of the heath in this respect and since as will be seen from what follows it would also lead to a steady decrease in acidity it might be expected to cause a degradation of the heath. Such has already been observed to be the case by Fritsch and Salisbury (**10**), so that the above results merely go to explain the facts already established.

The acidity of the surface layers after burning is invariably found to decrease, the mean results showing a change in pH from 3·2 to 3·5 (Table VIII). On the other hand the acidity of the deeper layers is found to increase slightly owing apparently to their more readily receiving the more acid leachings from the upper layers, as a result of which they become almost as acid as the surface soil. Burning thus leads to a general decrease in acidity, partly no doubt caused by the liberation of plant bases and partly by the destruction of organic acids. Since it is also evident that fires lead

to the destruction of much of the colloidal matter of the soil (see below), it is of interest to recall in this connection that McCool and Wheeting (**21**) found that artificial removal of the colloids from soil by Chamberland filtration led to a decrease in $H^{\cdot}$ concentration and a decrease in the amount of lime water necessary for neutralisation. The effect is probably due to the elimination of apparent acidity due to the selective adsorption of bases by the colloids, so the partial elimination of this effect by the destruction of colloids may possibly play a part in the lowering of acidity when the colloids are destroyed by fires. Burning also tends to equalise the acidity at different layers, a tendency which runs side by side with that towards equalisation of texture.

The coefficient of humidity appears to decrease somewhat both in the surface and 9-inch layers, but this is not shown in the 2-inch layers in the means owing to one anomalous result (4 BC). Neglecting this result it will be seen (Table VIII) that the salts/humus ratio as would be expected is increased considerably in the surface layers as a first effect though this condition is not maintained but regularly falls off with time (see Table X), while in the 9-inch layers the ratio decreases, probably owing to the increased exposure to washing out by rain. It is evidently this same factor which accounts for the salts/humus ratio falling off again in the 2-inch layers, though here it naturally takes longer to produce an effect than in the 9-inch layers owing to the greater amount of remaining humus. The retentive power of the surface layers is, however, so impaired as a rule by firing that they may show a continued loss of salts by leaching for as much as three or four years after the fire, and it is only after this time has elapsed and the soil is almost completely covered again by vegetation that the amounts of soluble salts again begin to increase, through the rate of production again coming to exceed that of loss. This is well shown in the case of the soils from 12 I and 2–3 Y in Table X, where there is seen to be a regular falling off of the augmented ratio value during successive years after the fire. This is undoubtedly due to the destruction of the soil colloids which are naturally not appreciably replenished until a fairly late stage in recolonisation. The destruction of the colloidal matter is clearly evidenced by the difference between the percentages of water retained in air by burnt and unburnt soils. The averages of 65 and 57 analyses respectively show that the mean values of this "hygroscopic moisture" for unburnt soil are 4·3 per cent. for the 2-inch layers and 1·3 per cent. for the 9-inch depths, whereas after burning the 2-inch layers only retain 0·65 per cent. and the 9-inch 0·9 per cent. Naturally again the greater difference is in the 2-inch layers since it is unlikely that any very marked direct effect of firing would be felt at the 9-inch depths.

Table IX. *Recovery from burning.*

Soil	Year of fire	Year of analysis	Water content 2″	Water content 9″	Humus 2″	Humus 9″	Total salts 2″	Total salts 9″	pH 2″	pH 9″	Salts/humus ratio 2″	Salts/humus ratio 9″	Interval after fire in years
12 I	1922	1922	13·8	10·5	3·5	1·2	1800	1075	3·8	4·6	515	895	½
4 XY	1920	1921	1·2	4·4	17·3	1·2	4540	1099	—	—	265	919	1
4 YZ	1920	1921	3·0	3·2	10·3	1·6	2380	552	—	—	231	345	1
4 4Z	1920	1921	70·6	8·1	50·5	6·4	7410	2667	—	—	147	417	1
12 I	1922	1923	10·2	7·9	4·2	1·2	1535	1019	2·9	3·7	365	814	1½
ML 0–9	1919	1921	7·6	7·0	17·6	3·9	3945	1179	—	—	233	328	2
4 XY	1920	1922	12·9	8·5	6·7	2·2	2320	1430	3·6	3·8	346	650	2
4 YZ	1920	1922	15·4	7·8	5·6	1·8	2500	1148	3·4	3·8	446	637	2
4 4Z	1920	1922	59·5	17·7	31·8	2·3	7400	2468	3·2	3·5	233	1073	2
2–3 Y	1920	1922	25·9	—	10·8	11·5	3840	1390	3·5	—	356	121	2
4–5 WX	1920	1922	25·8	6·0	10·2	2·4	6240	1850	3·2	3·9	611	770	2
3–4 YZ	1920	1922	4·1	7·5	3·2	0·6	1550	819	3·8	4·5	484	1366	2
ML 0–9	1919	1922	24·1	18·3	8·3	4·4	3577	2668	3·5	4·0	466	602	3
2–3 Y	1920	1923	8·3	—	9·3	—	2740	—	2·5	—	295	—	3
4–5 WX	1920	1923	—	—	0·6	—	2790	2125	3·6	3·2	4650	—	3
3–4 YZ	1920	1923	4·6	3·8	3·5	2·0	1678	950	2·9	3·0	480	475	3
2–3 Y	1920	1924	—	—	8·1	—	1560	—	4·0	—	193	—	4
3–4 YZ	1920	1924	—	—	—	2·0	—	615	—	4·0	—	307	4
36 B	1913	1921	15·4	—	41·8	—	6670	—	—	—	160	—	8
38 B	1913	1921	7·9	—	14·7	—	2598	—	—	—	177	—	8
40 B	1913	1921	12·9	—	21·2	—	4250	—	—	—	201	—	8
27 C	1912	1921	17·2	—	18·8	—	5880	—	—	—	313	—	9
28 C	1912	1921	9·4	—	18·7	—	3167	—	—	—	170	—	9
30 C	1912	1921	4·0	—	11·8	—	2172	—	—	—	184	—	9
36 B	1913	1922	21·8	—	9·4	—	3120	—	3·3	—	322	—	9
38 B	1913	1922	—	—	7·2	—	2560	—	3·6	—	356	—	9
40 B	1913	1922	—	—	11·6	—	6650	—	3·0	—	574	—	9
27 C	1912	1922	13·5	—	4·5	—	2525	—	4·1	—	561	—	10
28 C	1912	1922	21·9	—	10·6	—	2700	—	4·0	—	255	—	10
30 C	1912	1922	16·7	—	5·0	—	2170	—	3·8	—	434	—	10
36 B	1913	1923	8·6	—	12·2	—	3508	—	3·1	—	288	—	10
38 B	1913	1923	7·6	—	10·9	—	3770	—	3·1	—	349	—	10
40 B	1913	1923	34·7	—	15·6	—	5120	—	2·9	—	328	—	10
27 C	1912	1923	9·2	—	14·8	—	4255	—	2·5	—	288	—	11
28 C	1912	1923	3·5	—	5·7	—	1910	—	3·3	—	335	—	11
30 C	1912	1923	8·1	—	7·0	—	2220	—	3·0	—	317	—	11

Table X. *Leaching after burning.*

Soil	No. of years after fire	Salts/humus ratio 2″	Salts/humus ratio 9″
12 I	½	515	895
12 I	1½	365	815
2 – 2 Y	2	365	—
2 – 2 Y	3	295	—
2 – 2 Y	4	195	—

Table XI. *Recovery from burning.*

The table gives mean values for groups of soils from Table IX which are of the same age after burning.

Age of soil or interval after fire in years	Water content 2″	Water content 9″	Humus 2″	Humus 9″	Total salts 2″	Total salts 9″	Salts/humus 2″	Salts/humus 9″	pH 2″	pH 9″
½	13·8	10·5	3·5	1·2	1800	1075	515	895	3·8	4·6
1	24·7	5·2	26·0	3·1	4777	1437	214	559	—	—
1½	10·2	7·9	4·2	1·25	1535	1019	365	814	2·9	8·7
2	21·6	8·1	12·3	3·5	3971	1470	387	707	3·5	3·8
3	12·3	11·1	5·4	3·2	2696	1914	1473	538	3·1	3·4

Table XII. *Leaching on slopes after burning.*

		Salts/humus ratio						
Years after fire ...		1		2		9	10	11
	Soil	2″	9″	2″	9″	2″	2″	2″
Tops	4 XY	262	914	346	650	—	—	—
	36 B	—	—	—	—	332	228	—
	27 C	—	—	—	—	—	516	287
Middles	4 YZ	231	345	445	638	—	—	—
	38 B	—	—	—	—	365	349	—
	28 C	—	—	—	—	—	354	334
Bottoms	44 Z	147	416	233	1072	—	—	—
	40 B	—	—	—	—	573	328	—
	30 C	—	—	—	—	—	434	319

Table XII a.

Giving average values for the salts/humus ratio for high and low ground in two successive years of observation, calculated from the figures in Table XII, above.

	Salts/humus		Increase %		Leaching effect*	
	2″	9″	2″	9″	2″	9″
Means of all observations, 1st year	356	558	—	—	—	—
2nd year	325	787	-8·7	71·0	—	—
Tops, 1st year of observation	370	914	—	—	—	—
2nd ,,	307	650	-17·1	-28·8	-8·4	-100
Middles, 1st year ,,	313	345	—	—	—	—
2nd ,,	376	638	20·0	85·0	28·7	13·6
Bottoms, 1st year ,,	385	416	—	—	—	—
2nd ,,	293	1072	-24·0	158·0	-15·3	86·6

* = difference between actual increase and the mean increase shown in the first line of the table.

The general effects of leaching on burnt areas are roughly similar to those already described for unburnt areas as far as the surface layers are concerned, namely a loss of salts at the top of the slope and a gain at the base (cf. p. 49), as shown in Tables XII and XII a. Unlike the unburnt slopes, however (cf. Table VII f), the effect instead of being less at the 9-inch depths is far more marked than in the 2-inch depths, the 9-inch layers at the tops of the slopes losing in the aggregate 28 per cent. of their salts instead of gaining 71 per cent., so that the leaching effect is proportional to 100, and the 9-inch layers at the base acquiring double their original salt content. On more or less recently burnt slopes, as will be seen from the table (XII a), the 9-inch layers in the middles and at the bottoms of the slopes do increase in their salt content through leaching from the surface and 9-inch soils at the tops. All the normal effects are therefore as would be expected much more pronounced on the burnt than on the unburnt slopes, but the retentive properties of the surface soils are so impaired that even the lowest 2-inch soils here, unlike those on unburnt slopes, appear to lose more by leaching than they receive by drainage.

The means at the top of the table (XII a) show distinctly the gain here by the 9-inch layers at the expense of the 2-inch, but the gains by both

depths in the middles of the slopes appear to be almost without explanation. For some reason it appears that the middles were by far the poorest regions in salts before the fires so that on the increased supplies of drainage water they could themselves gain salts from above but at the same time pass on a solution sufficiently weak to cause further washing out of salts from the 2-inch depths lower down the slopes. A clue to the mechanism of this gain by the middles and simultaneous loss by the valleys immediately below may lie in the fact that the middles only receive drainings from one direction, and these may be very concentrated through the ready leaching from burnt ground above, whereas the valleys will be washed by larger quantities of drainage water from possibly three different directions, and this water, coming, as it may, in large part from ground that has not been recently burnt, is likely to be much more dilute than the solution received by the middles of the slopes.

To summarise then the effects of burning on salt content it may be said that the first effect is to increase the total salts present (see 12 AB in Table VIII and the abnormally high values at the beginnings of Tables X and XI). The added salts are then rapidly diminished by leaching (Table X) and the reduction continues until colonisation and the production of new humus check the process and cause the salts/humus ratio again to increase (Table XI). The decrease through leaching is much more pronounced than on unburnt ground, especially in the 2-inch depths in the valleys, and goes on for longer on the upper parts of the slopes than on the lower, the lower ground soon regaining salts through leaching from above. The lower ground would then perhaps be expected to be more hospitable for colonisation than the upper and as compared with older land would be more favourable for the development of deeper rooting forms such as *Calluna* and *Ulex nanus* (cf. Fritsch and Salisbury (**10**)) through the relatively higher salt content of its 9-inch layers.

RECOVERY FROM BURNING.

The process of recovery from burning is best illustrated by Table XI which gives the mean results calculated from the data in Table IX. In this table (XI) averages have been taken for all soils of the same age since the last fire (i.e. with which equal intervals have elapsed since last being burnt). It shows a gradual increase in acidity during the first three years from a *p*H of 3·8 to 3·1 in the 2-inch layers and from 4·6 to 3·4 in the 9-inch layers and also serves to illustrate the march of changes in the salts/humus ratio. After the first few months the ratio is still high but falls to a minimum about the end of the first year, after which it again regularly increases. This is well seen in the 2-inch depths but is not so distinct in the 9-inch, as the last two values appear too low. The increase in the actual quantity of humus is best realised by comparing the percentages shown in the 1922 and 1923 analyses

of soils from 36 B, 38 B, 40 B, 27 C, 30 C, 12 I and 3–4 YZ (see Table IX). As would be expected the increase is a general phenomenon in recovering soil, the relatively few examples which may be found in the tables where the reverse appears to take place (e.g. 28 C and 4–5 WX) being fully explained by incidental causes such as reburning, but some of these cases will be discussed later.

Effect of Height on Slopes.

Results have been collected in Table XIII to show the variations in water content, humus content, total salts and acidity at different heights on slopes. In each group of figures the top line gives the value for tops, the next the intermediate value or values at half way heights and the bottom one the figures for the valleys. It will be observed that the water content is almost invariably considerably greater at the bottoms of the slopes than on the tops but that general rules cannot equally well be laid down for humus content, acidity or content of total salts. With respect to humus the figures are not at all diagrammatic but show few exceptions to the general rule that there is usually distinctly more humus in the valleys. That this is the general rule is clearly brought out by the means shown at the end of the table (XIII), which it will be seen bear a fairly good relation to the individual cases, and also by a comparison of the humus contents for tops and valleys already given in Table VII d. In Table XIII also the aberrant figures are readily explained by the differences in the character of the vegetation at the different heights which are brought about by the erratic nature of some of the past fires. Other things being equal, i.e. with the same association at the same stage throughout the whole slope, there is more humus in the valleys as brought out by the groups of figures in Table XIII, the bottom figures in these groups being usually greater than the top ones.

The total salts are usually greater in the valleys than on the tops, this point being shown both by Table XIII and Table VII. The reason appears to be twofold: firstly, the higher water content (see Table VII) favours a more luxuriant growth and a greater formation of humus and secondly, the low ground, as established in Table VII f, receives leachings from the higher.

In the case of acidities the gradient may be either upwards or downwards, i.e. the upper part may be more acid than the lower or *vice versâ*. Acidities on slopes cannot therefore be said to run side by side with water content or humus, but the determining factor appears to be the nature of the valley vegetation, which is more variable than that of the summits. It will be seen from the table (XIII) that the mean results show a greater acidity in the valleys and that this also holds in six out of the nine individual cases. It has been shown by Conner ((**5**) and (**6**)) that soils rich in organic matter showed greater acidity when fully saturated and those low in organic matter were more acid when only half saturated, so that if differences in the water and humus contents were responsible, it appears that the opposite relation

Table XIII. *Variation of properties with height of slope.*

Slope	Age of vegetation in years	Water content 2″	Water content 9″	Humus 2″	Humus 9″	Total salts 2″	Total salts 9″	Coefficient of humidity 2″	Coefficient of humidity 9″	Salts/humus ratio 2″	Salts/humus ratio 9″	pH 2″	pH 9″
F 1, 36 B	9	21·8	—	9·4	—	3120	—	2·5	—	332	—	3·3	—
F 1, 38 B		—	—	7·2	—	2560	—	—	—	355	—	3·6	—
F 1, 40 B		—	—	11·6	—	6650	—	—	—	573	—	3·0	—
F 2, 27 B	10	13·5	—	4·5	—	2325	—	3·0	—	516	—	4·1	—
F 2, 28 B		21·9	—	10·6	—	2700	—	2·1	—	255	—	4·0	—
F 2, 30 B		16·7	—	5·0	—	2170	—	3·3	—	435	—	3·8	—
Valley A, west, 4 line	2	12·9	8·5	6·7	2·2	2320	1430	1·9	3·9	346	650	3·6	3·8
		15·4	7·8	5·6	1·8	2500	1148	2·8	4·3	446	638	3·4	3·8
		59·5	17·7	31·8	2·3	7400	2468	1·9	7·7	232	1072	3·2	3·5
Valley B, west, 4 line	6	10·8	7·0	4·5	0·5	2350	627	2·4	13·8	522	1254	3·0	4·3
		18·6	13·4	1·7	3·0	2895	2220	1·1	4·4	1700	740	3·5	3·8
		13·4	15·2	14·9	2·6	2172	2172	0·9	5·9	146	835	3·9	4·2
		12·5	16·2	4·6	2·8	2102	2322	2·7	5·8	456	828	3·9	4·0
Erica slope	8	21·9	—	16·0	1·25	5700	1098	1·4	—	356	878	3·1	3·4
		11·2	5·9	5·1	2·45	2560	1050	2·2	2·4	505	428	3·2	3·8
		27·0	9·3	25·2	3·14	5000	1885	1·1	3·0	199	600	3·3	3·3
		39·7	8·5	28·3	3·7	6250	1910	1·4	2·3	221	515	3·3	3·7
Opposite *Erica* slope	7	34·8	34·3	16·3	1·9	4540	1665	2·1	18·0	278	875	3·5	4·0
		14·8	5·7	2·2	0·6	1784	533	6·6	9·5	810	888	3·4	4·0
		—	8·2	—	6·1	—	1430	—	1·3	—	234	—	3·7
		29·5	102·5	10·1	2·4	3635	1480	2·9	42·7	360	615	3·4	3·3
		92·1	25·6	5·07	4·3	4030	2500	1·8	6·0	795	581	3·8	4·1
Valley A, east, on the 4 line	6	20·7	—	8·9	2·9	3920	1072	2·3	—	440	370	3·2	3·6
		16·6	6·8	36·8	2·2	3032	1340	0·5	3·1	82	610	3·4	4·0
		13·5	6·8	5·6	0·6	2320	793	2·4	13·0	414	1320	3·1	3·6
		30·25	10·6	11·9	2·2	3920	1350	2·5	4·8	330	613	3·2	3·9
		59·5	17·7	31·8	2·3	7400	2468	1·9	7·7	232	107	3·2	3·5
Valley B, west, on the 12 line	Over 15	7·1	21·8	2·6	7·7	1885	3030	2·7	2·8	725	394	3·9	3·2
		10·1	7·6	2·3	—	1428	722	4·4	—	620	—	3·8	4·3
		18·5	9·5	7·1	3·4	2752	1738	2·6	2·8	387	510	3·5	3·5
		41·7	9·5	17·8	2·3	6450	2630	2·3	4·1	363	1144	2·9	3·8
Valley A, east, on the 12 line	Over 15	64·7	8·3	21·9	1·04	5710	1000	3·0	8·0	251	960	3·2	4·2
		41·7	—	36·4	—	6666	—	1·1	—	183	—	3·3	—
		89·4	26·6	97·9	9·6	10000	4760	0·9	2·8	102	496	2·9	3·1
		133·5	20·7	92·8	8·4	18150	425	1·4	2·5	195	506	2·9	4·1
Means: All tops		23·1	16·1	10·1	2·5	3451	1417	2·3	7·1	418	767	3·4	3·8
Intermediates		24·8	18·6	17·5	3·1	3430	1615	2·3	8·8	481	656	3·4	3·64
All bottoms		56·9	16·6	25·4	3·7	6820	2103	2·1	5·2	390	679	3·3	3·8

should hold and that the greater acidity should be found on young heaths at the tops and on old heaths in the valleys, where there is a higher water content. Thus in old ground acidity and water content should run parallel, if the rule applies, and the greater acidity be found in the valleys, while shortly after fires the reverse should be true, but such is not the case (see especially Valley A, west, 4 line in Table XIII). The effect is therefore apparently not merely related to the water content or humus, but depends as suggested above upon the nature of the vegetation at the bottom of the slope. It is significant that in the three cases where the valley was found to be less acid, the base of the slope was occupied by a special zone of *Ulex europaeus* and *Pteris*. A particularly well marked zone of this type existed also at the junction of the valleys A and B round 20–21 YZ and special samples from this region showed that such zones were associated

with a lower acidity, the pH being only 3·9. This appears to be the explanation of the lower acidities at the bases of the three slopes in question, viz. valley B, west, 4 line, the *Erica* slope and opposite the *Erica* slope. The last named is particularly suggestive, as the type of vegetation here only changed at the very base and it is accordingly only the last pH value going downwards which shows the decreased acidity, the intermediates showing the normal tendency to rise towards the valley.

In the six cases which obey the rule of higher acidity in the valley it is further to be observed that the effect is very much more pronounced in the case of the oldest vegetation such as that of the 12 line slopes at the bottom of the table than in the younger slopes. This may be related not only to the direct effect of the greater percentages of humus on these slopes, especially at the bases, but also to the fact that less drainage appears to take place on the old ground than on the young, so that the valley acidity would be less ameliorated by washing through with drainage water than it appears to be on the younger slopes. The drainage effect and washing out of the valleys evidently decrease markedly with increasing age of the vegetation. Owing to the accumulation of large quantities of humus water is retained instead of being allowed to wash out the lower layers and is re-evaporated from positions high on the slopes. This theory that there is less travel of drainage water down the slopes on old ground is supported by the figures given in Table VII h for the changes in the salts/humus ratio at the top and bottom of the 12 line slope between 1921 and 1922, which testify to the lack of drainage effects here as compared with other slopes. It will be remembered that in the aggregate (Table VII f) the salts/humus ratio increased for 2-inch depths by 38 per cent. in the year, but after the wet season had increased in the valleys more than on the tops owing to the washing of salts down the slopes. Here, however, there is no general increase (Table VII h), probably because the zone was already so old as to have reached a state of equilibrium. It therefore only shows a loss of salts from the 2-inch layers to its 9-inch depths, and in the valley the salts/humus ratio has actually fallen off rather more than on the top, showing the lack of drainage effects down the slope. Possibly the gradual elimination of this drainage effect with vegetation of increasing age may be a factor favouring the development of a much higher acidity in the valleys as compared with the tops.

Experiments on the Percolation of Water and Salt Solutions through Burnt and Unburnt Soils.

It has been assumed in a number of connections in the foregoing sections that a soil after burning would more readily allow water and salts to drain through it than an unburnt soil, and that in consequence salts would be more readily leached on burnt areas and would be more readily drained to the lower levels of a burnt slope than an unburnt.

It seemed advisable therefore to make a few laboratory experiments upon burnt and unburnt soils to establish that this is actually the case. Experiments have therefore been carried out on the permeabilities of different samples of water and salts, the permeability of the unburnt soil being found first and then compared with that either of a natural burnt soil or a soil artificially slowly heated until the organic remains appeared to be charred to approximately the same extent as is found in the field shortly after a fire.

The Percolation Rates with Water.

The permeability to water was roughly determined by finding the time required for the water level in a long glass tube of 3 cm. diameter and containing a column of soil 20 cm. high supported on gauze at its lower end to rise 10 cm. under a pressure of 20 inches of water. The soil was in all cases very carefully packed into the tube and as uniformly as possible, the final pressure used being always that which would just cause the column to slide in the tube. The upper limit of the column was defined by a piece of gauze supported by a glass rod so as to keep the packing uniform and the column the same length. The method is admittedly very rough but seemed sufficient for the present purpose and the values as given below are sufficiently different to be significant. The times taken were as follows:

	Unburnt soil		Collected burnt soil		Artificially burnt soil	
	5 mins.	5 secs.	1 mins.	46 secs.	0 min.	43 secs.
	3	43	2	0	—	—
	4	37	1	26	1	0
	4	30	—	—	—	—
	8	10	2	0	0	43
	11	40	0	44	—	—
	11	50	0	50	1	0
Means:	7 mins.	4 secs.	1 min.	20 secs.	0 min.	54 secs.

It is then evidently quite legitimate to assume that drainage is much facilitated by burning whether in the laboratory or in the field.

Rates of Drainage of Salts.

The leaching and drainage rates of burnt and unburnt soils collected from about 2–3 X were compared by the following method. A column of soil 20 cm. high, carefully and uniformly packed as in the determination of percolation rates (see above), was supported by a piece of wire gauze resting on the inturned edge of a glass tube 3 cm. in diameter and 50 cm. long, the soil having been air-dried and crumbled before packing. The tube was marked at 10 cm. above the soil level (the volume of the tube between the top of the soil and the mark being roughly 66 c.c.). The soil was then thoroughly washed through from above with tap water at a constant head of 10 cm. for half an hour until the water draining through had a constant conductivity. The resistance of the drainings was measured at intervals and it was found,

as would be expected, that their concentration was greatest at first and fell off with time but that with unburnt soil it eventually fell to about half the concentration of the tap water which was being supplied at the top. The soil therefore gives up electrolytes to the washings at a decreasing rate but in the end must be absorbing electrolytes from the in-going solution. The reason for this behaviour is not altogether clear, but it suggests either that the tap water happens to contain electrolytes which are more readily absorbed by the soil than are the substances which were originally present, or that some substance in the tap water forms a compound with something present in the soil which is either insoluble or less dissociated.

When the drainings reached a constant conductivity the liquid over the soil was allowed to drain just to the soil level and replaced by 50 c.c. of 1 per cent. Tidman's sea salt solution with which the tube was kept filled to the mark by means of a dropping funnel supported above. The emerging solution was allowed to fall into 1000 c.c. of distilled water in a reservoir below and the rate of increase of conductivity of this water was measured by successive readings for half an hour, the rate of increase being taken to give a measure of the facility of salt-drainage through the soil.

After half-an-hour the salt solution was allowed to drain to the soil level and the tube was again kept filled to the mark with tap water. The conductivities of successive five minute fractions of "leachings" were then measured to find the rate or the facility with which the salts could be washed out. The results are set out in Table XIV and plotted in Fig. 3.

The results indicate that although the burnt soil showed more absorption at the very beginning, its leachings coming out initially less concentrated than those from the unburnt soil, it allowed its leachings continuously to increase in concentration for 15 minutes and then only retained sufficient salts from the tap water to reduce the concentration of the latter by 15 per cent., whereas the unburnt soil allowed no increase in the concentration of its leachings from the beginning, absorbed electrolytes from the tap water continuously from the fifth to the 107th minute after the start and reduced its concentration to 53 per cent. It might be argued that the conductivity of the leachings from the burnt soil is still high at the end of half-an-hour because it has only been giving up its salts slowly, and that that from the unburnt soil is already low because it has lost all its salts quickly and has no more to lose. If, however, this were the correct interpretation, obviously the values of the resistance of the solution from the burnt soil should have been *rising* to their final value and those of the unburnt soil should have been falling. The reverse is true in both cases so evidently the first interpretation is the correct one and the unburnt soil is the more retentive of absorbed salts.

In the second part of the experiment it is seen that in equal times the burnt soil allowed $2\frac{1}{3}$ times as much water to pass as the unburnt soil and

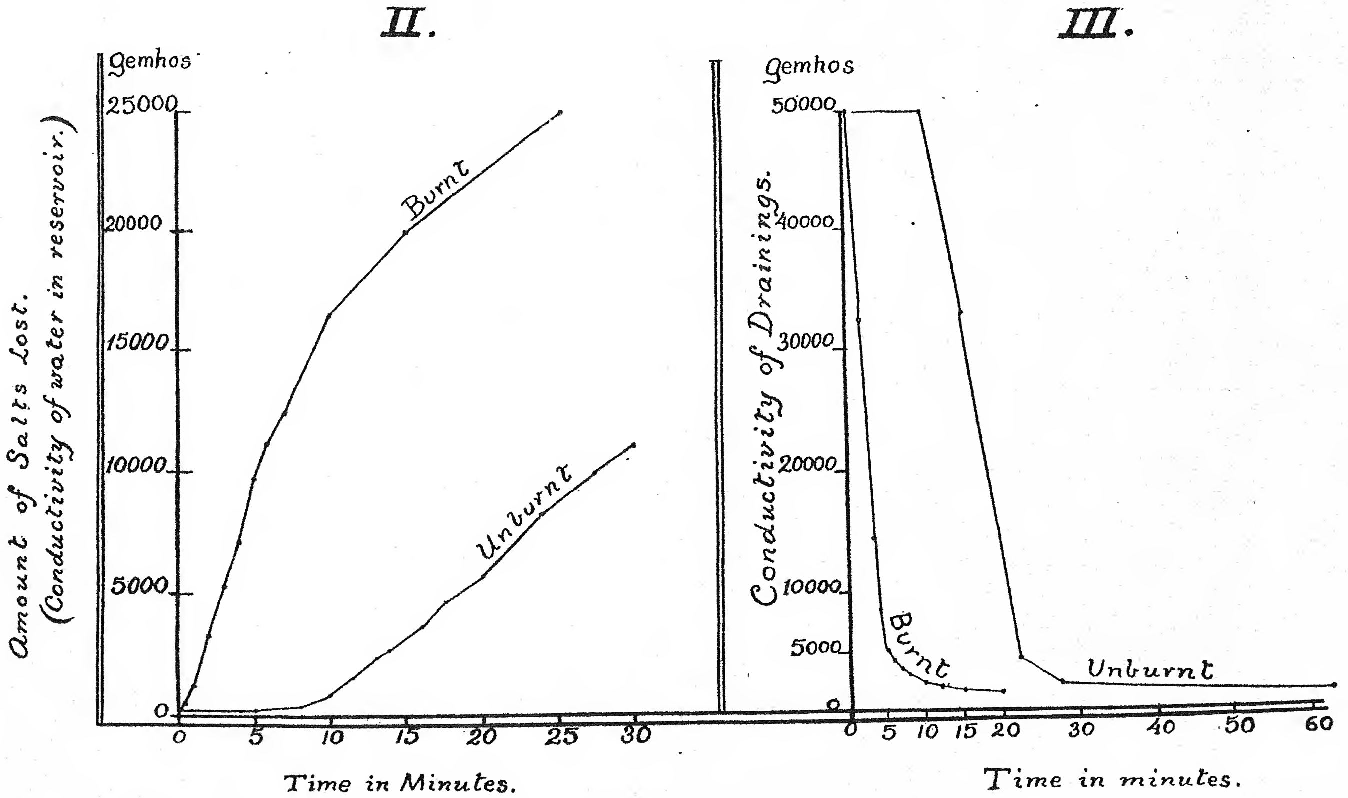


FIG. 3. Results of experiments on the rates of drainage of water and salts through burnt and unburnt soils. The first part of the experiment is not plotted. II shows the greater rate of passage of salts through burnt than unburnt soil. III shows that when a burnt soil and an unburnt soil are impregnated with salts and then washed through with water the concentration of the drainings falls very rapidly in the case of the burnt soil as all the salts are very rapidly washed out, but that with the unburnt soil the conductivity remains high for a much longer time as the salts are less rapidly removed. (The drainings here are smaller in quantity.) For further explanation see text, pp. 59–62.

Table XIV. *Experimental results on the rates of drainage of water and salts through burnt and unburnt soils.*

(I) First extraction with tap water			(II) Rate of drainage with 1 % Tidman's sea salt solution			(III) Washing out of sea salt with tap water		
	Resistance of the drainings in ohms			Resistance of the water receiving leachings in ohms			Resistances in ohms of the successive fractions of the drainings	
Time in mins.	Burnt soil	Unburnt soil	Time in mins.	Burnt soil	Unburnt soil	Time of collection of fraction (minutes)	Burnt soil	Unburnt soil
1	690	515	0	10,000	10,000	¼	20	—
2	660	525	½	2,060	—	½	20	—
5	660	550	1	880	10,000	1½	30	—
6½	670	—	2	300	—	2	—	20
10	665	720	3	190	—	3	70	—
13	640	—	4	140	—	4	120	20
15	650	880	5	110	10,000	5	195	20
20	650	—	6	90	—	6	240	—
25	650	—	7	80	—	7	288	—
40	—	—	8	—	3,220	8	340	—
50	(560 c.c. passed)	975	10	60	1,040	10	410	20
65	—	—	11½	—	630	12	470	—
74	—	980	13	—	430	15	535	30
82	—	990	14	—	360	20	600	—
86	—	990	15	50	—	20–25	—	220
95	—	990	16	—	260	25–30	—	400
107	—	1030	17½	—	210	60–65	—	640
117	—	1030	20	—	170	—	—	—
—	—	(650 c.c. passed)	24	—	120	—	—	—
—	—	—	25	40	—	—	—	—
—	—	—	27½	—	100	—	—	—
—	—	—	30	40	90	—	—	—
—	—	—	—	(360 c.c. passed)	(155 c.c. passed)	—	—	—

allowed as much salt to be washed through in six minutes by 72 c.c. as the unburnt soil in 30 minutes by 155 c.c. (viz. enough to bring down the resistance to 90 ohms). It therefore appears to be about five times as efficient in allowing salt drainage, so far as rate is concerned, and to require less than half the amount of water to remove the same amount of salts.

The third part of the experiment, dealing with the washing out of the salts contained, shows that the rate of washing from the burnt soil is about 50 times the rate from the unburnt soil, the percentage increases in conductivity over given equal intervals (e.g. the first 15 minutes) being respectively 50 per cent. for the unburnt soil and 2675 per cent. for the burnt. The time required for the first signs of change in conductivity in the case of the burnt soil is also only a tenth of what it is for the unburnt, so that it may be safely concluded that leaching and drainage on slopes in nature are considerably facilitated by burning.

The Soil Properties of Special Zones and in Relation to Special Ecological Features.

The relation between the properties of the soil and the ecological characteristics of the vegetation growing upon it are brought out by Table XV which has been constructed from the analyses of several soils from each type of zone, each soil being analysed in three different years and the results averaged together. The method of making these averages should preclude the possibility of the differences in the figures being due to seasonal variations or other irrelevant causes. The figures explain themselves and the table is easily read but attention may be drawn to one or two of the points which it shows. Fritsch and Salisbury (**10**) have pointed out that some years after firing the vegetation normally attains a phase in which *Calluna*, *Ulex nanus* and *Erica* are simultaneously dominant. This may be taken to be the average condition of the heath and is extensively represented. (It will be alluded to here, as in Fritsch and Salisbury's paper, as *C.U.E.*)

Table XV. *Averages for soils from special zones.*

Zone	Water content 2″	Water content 9″	Hygroscopic moisture 2″	Hygroscopic moisture 9″	Humus 2″	Humus 9″	pH 2″	pH 9″	Total salts 2″	Total salts 9″	Coefficient of humidity 2″	Coefficient of humidity 9″
Average *Calluna-Ulex-Erica*	18·7* (65)*	8·16 (57)	4·3 (48)	1·3 (49)	14·2 (50)	2·2 (48)	3·42 (38)	3·9 (39)	3825 (63)	1455 (63)	1·3 (65)	3·3 (57)
Vaccinium (7)†	43·3	7·2	5·1	3·7	36·0	2·2	3·2	3·5	7879	1383	1·2	3·3
Molinia (7)	42·7	12·4	5·8	3·4	24·1	12·6	3·30	3·36	5881	2144	1·8	1·0
Aira, 25 B (2)	10·4	8·3	2·3	1·6	4·7	1·5	3·5	3·7	2162	1525	2·2	5·5
Burnt areas on west side of Valley B with:												
Ulex nanus (3)	5·4	5·1	1·8	0·6	3·7	1·0	3·3	3·7	1793	750	1·5	5·1
Erica cinerea (3)	7·1	2·0	1·9	0·2	13·4	5·3	3·0	3·8	3159	1427	5·3	3·8
Pteris aq. (3)	19·7	3·9	4·4	0·4	5·6	1·7	3·4	3·6	4765	1715	3·5	1·9
Poor *Calluna* (25 O–Z) (1)	2·3	—	0·1	—	4·0	—	2·9	—	1368	—	0·6	—
Erica tetralix (4)	21·2	14·7	2·4	2·9	11·5	5·2	3·3	3·8	3466	2700	1·8	2·8
Gravel (4–5 J) (2)	11·1	11·8	2·2	2·1	2·0	1·7	4·0	3·8	1795	1880	5·5	6·9
Burnt areas	8·0 (24)	7·8 (4)	0·65 (24)	0·9 (4)	8·6 (24)	1·9 (4)	3·5 (16)	3·65 (4)	2664 (24)	864 (4)	0·9 (24)	4·1 (4)

* The values are based on all appropriate samples taken in 1921, 1922, and 1923, the number of determinations which have been averaged being given by the figures in brackets in each case.

† Figures in brackets in this column apply to the whole line.

Table XVI. *Figures taken for comparison from paper by H. Jeffreys* (**16**).

	Water content	Humus	Coefficient of humidity	Acidity as given (=c.c. $N/10$ acid/100 gm. soil)	Acidity expressed as pH of 50 gm./20 c.c. extract
Callunetum	60·7	25·3	2·4	4·94	2·91
Pteridetum (1)	17·0	7·0	2·4	1·6	3·4
(2)	21·4	6·7	3·2	1·8	3·35
Molinietum	77·1	12·2	6·3	2·86	3·15

The first row of figures (Table XV) is for such average *C.U.E.* and is based on a fairly large number of samples, the numbers of readings used in obtaining the means being given in brackets. The readings for special zones may all be compared with these means in deciding whether they are abnormally high or abnormally low in any particular respect.

Soils on which *Vaccinium* is a prominent feature are characterised by being very rich in surface humus and soluble salts and possessing a high water content, but whether the high water supply or the richness of the soil is the more important factor there is nothing to suggest. *Vaccinium* is tolerant of a high degree of acidity, being associated with soils which are unusually acid both in their 2-inch and 9-inch depths, the respective *p*H's being 3·2 and 3·5. It is more so apparently than any other species mentioned with the exception of *Erica cinerea*. *Vaccinium* can support an acid soil provided it be very wet but *Erica* will become dominant on a still more acid soil when the water content is very low. The figures for *Erica* in the table are those for a specially well marked zone on the west side of valley A. The valley slope here had been burnt in 1920 and showed in 1921, 1922 and 1923 along this side three very obvious, well-marked and distinct zones, the boundaries between them running at right angles to the direction of the valley, of which the first was dominated by *Erica*, the second by *Ulex nanus* and the third by *Pteris*. In each case the dominant constituted quite 80–90 per cent. of the vegetation in the three years mentioned though they were becoming less marked in 1924. Similar zonations were observed here by Fritsch and Parker in 1913 and are figured in Fig. 1 of their paper (**9**). The figures for each of these zones are recorded in the table (XV) as burnt areas with *Erica*, *Ulex nanus* and *Pteris* respectively. The zone with dominant *Erica* shows with one exception for its surface layers the most acid mean *p*H in the table, though the 9-inch depth is almost as alkaline as any. In this *Erica* zone then there is a greater difference between the acidities of the 2-inch and 9-inch depths than in any other situation and the fact, though it does not go in any way to explain the zonation, is probably significant in connection with the rooting depths of the plants concerned. *Erica* as shown by Fritsch and Salisbury (**10**) is comparatively shallow rooting, but in the case of the zones dominated by plants which penetrate more deeply such as *Ulex nanus* and *Pteris* there is a far less marked difference between the acidities of the 2-inch and 9-inch layers. There is least difference in acidity with the *Pteris* which penetrates most deeply. Of the three zones the *Erica* is the most acid, the *Ulex nanus* next and the *Pteris* zone the least, but the salt and humus contents do not run in the same order. In the case of the "*Erica* slope," for which figures have already been given in Table XIII, the degree of acidity is slightly less and the water content considerably higher.

Definite *Molinia* zones appear to be characterised by high acidity

(pH = 3·5) and to be almost as acid at the 9-inch depths as at the 2-inch (mean pH = 3·36), in which feature they stand apart from all other cases. This is evidently related to the fact that the soils are altogether very rich in humus and that the 9-inch depths are particularly exceptional in this respect. If the figures for the *Molinia* zones in Table XV be compared with the average value of the two years means for valleys in general given in Table VII d, which here will form the fairest "control" for comparison, it will be seen that the water contents, the total salts and the 2-inch humus are large but all very close to the mean values for valleys, but that the 9-inch humus content is 12·6 per cent. against a mean value of 3·8 per cent., or over three times the normal. This probably explains the exceptionally high acidity at the 9-inch depths as compared with the 2-inch, and is evidently related to the fact, to which attention is drawn by Jefferies (**14**), that *Molinia* penetrates deeply into the sub-soil and possesses root hairs at all levels, so that more than the average amount of humus would be formed in the deeper layers. The coefficients of humidity are decidedly less in the *Molinia* zones than the average values for valleys, not apparently because there is a smaller water content but because there is more humus (cf. "sponge-like" action of the humus referred to above, p. 47). It is also to be remembered, however, that some of the *Molinia* zones were not actually in valleys, so this comparison with valley means, though useful in a general way, may not be altogether just.

The results for *Molinia* zones fall well into line with the observation of H. Jeffreys (**16**) that "*Molinia* usually grows where there is a large amount of humus in the soil and the water supply is peaty in character," but whereas Jeffreys found the Callunetum to possess a still higher acidity than the Molinetum, in the present case the reverse is true. It is interesting to compare the figures for the water content, humus, coefficient of humidity and acidity of the general *C.U.E.* vegetation and *Molinia* and *Pteris* zones with some of those given by Jeffreys. Some of the latter are quoted in Table XVI. Jeffreys' results for acidity were found by titration and given in c.c. of $N/10$ acid per 100 gm. soil, so, for the purpose of rendering them roughly comparable with the writer's results, they are in Table XVI also converted into the pH values which would have been given by a 5 gm. : 20 c.c. extract, assuming the acid to be completely dissociated. (This assumption is not strictly legitimate owing to the weak nature of the acids concerned, but will serve for a rough comparison.) Comparison of Tables XV and XVI shows that although the formations studied by Jeffreys were all much wetter than those of Table XV, the Callunetum in particular being also much richer in humus, some of the results are strikingly similar. In the *Molinia* zones the pH's compare as closely as 3·15 and 3·3, and the humus contents found by Jeffreys fall between the 2-inch and 9-inch values recorded by the writer. The Pteridetum also agrees very closely, the typical water contents being 17 and 21 per cent. against 19·7 per cent., the humus 7 and 6·7 per cent. against 5·6 per cent., the co-

efficient of humidity being 2·4–3·2 against 3·5 and the acidities identical at a pH of 3·4. Salisbury, however (**25**), finds in the case of woodlands on Hythe beds (like the present soils) a pH for *Pteris* of 4·9 and for *Vaccinium* of 4·4 against the present record of 3·2.

Soils from the *Molinia* zones frequently showed evidence of peculiar properties during the determination of their acidities. The extract has the capacity of frothing very much like a solution of egg albumen so that a row of films is formed by the bubbles of hydrogen passing through the electrode vessel. Another peculiar property is that the solutions from these zones, after coming to a sort of transitory equilibrium on saturation with hydrogen and giving a pH reading of a normal order, were found to possess the capacity of "creeping" up to a higher and higher pH if the passing of hydrogen were much prolonged. Some of the *Molinia* zone solutions would creep in this way until showing an E.M.F. which corresponded to a pH of 9 or even 10 but nothing could be made out concerning the cause of the phenomenon. It was certainly due to some special substance or substances present in the soil extract and was not an artifact, since every possible precaution was taken and the phenomenon was persistently exhibited with different electrodes, different sources of hydrogen, different extracts of the same sample and so on, but the nature of the substances which cause it has not been determined. Bicarbonates might cause a slight creeping through washing out of CO_2 but could not account for an effect of the order observed. The effect was only exhibited with extracts from definite *Molinia* zones (e.g. those round 20 C, 19–20 C and at point O), except that it was also found in soils from gravel patches at 4–5 J, one soil from near the junction of the valleys A and B close to a definite *Molinia* zone, and a position in the *Erica* zone on the west side of valley A, in all of which localities *Molinia* occurred to some extent. Other samples estimated alternately with them came quickly to a final equilibrium in the normal way. The apparent association of the phenomenon with *Molinia* may of course be only incidental but seemed worthy of record.

In the case of the *Aira* (*Deschampsia*) zone for which figures are recorded in Table XV the peculiarities must be found by comparison with the figures given for Middle Line tops in Table VII. These figures were obtained from soils in topographically comparable situations. *Aira* (*Deschampsia*) *flexuosa* is of restricted distribution on the heath and is seldom abundant, but becomes a prominent feature in this particular zone at 25 B. By comparison with the control mentioned above it will be found to be relatively poor in humus and salts and to be below the mean acidity.

Erica tetralix forms well defined zones in certain places on the heath, the most remarkable being at 0 B and in the region of 3 J where it thrives almost to the exclusion of everything else. The soil is of more than average acidity in the surface layers but like that of the *Erica cinerea* zone of valley A already mentioned is almost as alkaline as the average at the 9-inch depths. As

already suggested this may again be associated with the relatively shallow rooting. The content in soluble salts is also exceptionally high for the deeper layers.

Special zones of *Triodia decumbens*, which is also of very restricted distribution, occur on the heath but so far as all that have been sampled are concerned they coincide with those of *Erica tetralix*.

At the end of the table (XV) figures are given for almost bare gravel patches on the land-slides at 4–5 J (see map) and for freshly burnt areas. The properties of burnt areas have already been fully discussed but the figures are interesting for comparison. The surface soil is less acid than that of any of the others except the bare gravel which is the most alkaline of all. Its frequent early colonisation by *Molinia* (cf. Fritsch and Parker (**9**)) therefore becomes at first rather surprising since *Molinia* is normally associated with high acidity. This, however, appears to be rather a manifestation of tolerance than of preference and the association of *Molinia* with lower acidity when not in a definite somewhat marshy "*Molinia* zone" is also well seen in its distribution along the 4 line (see Table II a), where it will be seen to coincide with the least acid zones. T. A. Jefferies (**14**) also observes that *Molinia* has a varied habitat, being associated with acid soils but also occurring in low-lying fens which are calcareous or neutral. It is therefore evidently tolerant of a wide range but in the present case is only associated with lower acidity when there is relatively little competition. It is at first a little surprising perhaps that the 9-inch layers of the bare gravel should be more acid than a corresponding depth of a soil bearing average *C.U.E.* The fact can only be attributed to the circumstance that the gravel, being nearly bare, is not subject to fires, so escapes their influence in periodically replenishing the supply of bases and reducing the acidity. It is of course also subject to the reception of acid drainings from *C.U.E.* higher on the slope.

The "Poor *Calluna*" zone at 25 25 Z is a small area which has stood out for many years as a zone of extremely poor vegetation, on which the soil has never become fully covered and bears practically only very poor *Calluna* plants which rarely exceed 5–6 inches in height. It will be observed that it is very poor in humus and especially in colloids as shown by the air-dry water content. It is also very poor in salts and the acidity is extraordinarily high (2·9). The reason for these characteristics is not apparent.

Bare patches. It has been observed that on fired areas definite bare patches may persist for many years after all the surrounding soil is again completely covered with vegetation. Samples have accordingly been taken from such bare patches and from under the surrounding vegetation with a view to determining the differences to which they are due. Only two sets of determinations have been made in this direction and these are given below but it cannot be said that they shed very much light on the question. The bare

patches appear in the aggregate to be more acid than the surrounding soil though possessing less humus and being less rich in salts, but the results are not at all definite and too few determinations have been made.

	Salts	pH	Humus
Bare patches	1490	3·4	9·4
	2325	3·3	7·8
Controls	3275	3·4	44·2
	1018	3·65	7·6

Analyses for Potassium and Aluminium.

In a few cases potassium and aluminium were estimated with the object of determining the relative amounts of soluble potassium on burnt and unburnt ground and on the tops and in valleys and of finding out whether the aluminium content bore any relation to the degree of acidity. Estimations were made on four samples from tops and on five from valleys, but the results were not sufficient to lead to any conclusions. The figures showed no relation between acidity and aluminium content, nor apparently does any relation exist between the contents in either potassium or aluminium and topographical position. An attempt has been made already by Burgess (**4**) to correlate aluminium contents and acidities in acid soils, but whereas some parallel could be observed when the soils were taken in groups, the mean aluminium content (388 ppm.) of soils with a pH more acid than 5 being greater than that (26 ppm.) of soils with a more alkaline pH than 5, there was, as here, no regular parallel in the individual cases. The percentages of potassium average roughly the same both for tops and valleys and in the main run parallel with the percentages of humus. If any of the soils investigated had been sampled at very short intervals after firing, for reasons already put forward under the effects of fires, it seems probable that even this rough relationship would not have been obtained.

SUMMARY

A systematic soil survey has been undertaken of the area on Hindhead Common indicated in the accompanying map and defined by Fritsch and Parker (**9**).

Samples were taken at 100 feet intervals along certain transects across the area, and from certain special zones of which the vegetation showed characteristic features, and were analysed for humus, water content, hygroscopic moisture, acidity, calcium, nitrates, total salts and in a few cases aluminium and potassium.

The paper deals with the effects of wet and dry seasons, leaching and drainage effects on slopes, the effects of fires, leaching on burnt ground, the process of recovery from burning, the alterations in some physical properties of the soil on burning and the soil characteristics of special ecological zones.

The first characteristic of the soils in general is their very high acidity, the mean pH for an extract of 5 gm. soil in 20 c.c. of water being 3·4 for

2-inch depths and 3·9 for 9-inch depths. The 9-inch depths are almost invariably less acid than the 2-inch. The range of pH is 3·9–2·3 for 2-inch depths and 4·7–3·1 for 9-inch depths.

In dry and wet seasons the greatest variations in the coefficient of humidity are found in surface layers on high ground and the least variations in surface layers in the valleys. The 9-inch depths are intermediate, the tops again varying more than the valleys. On old ground a wet season leads to a loss of salts by the tops and a considerable gain in the valleys. 9-inch layers, however, do not gain at the expense of the 2-inch layers.

Fires lead to the destruction of 60 per cent. of the original humus in relatively young heath but only about 30 per cent. in older heath, where the soil is particularly rich in humus. The colloidal properties of the organic matter which remains are always much impaired. Drainage of salts into the valleys becomes more pronounced, and the 9-inch layers in the valleys at least do now show a considerable increase at the expense of the salts lost by the high ground and surface layers. The total salts are at first increased but are then rapidly leached out until well below normal. They continue to fall through further leaching until a late stage in recolonisation (possibly for six to eight years), when sufficient new humus is formed to check the process. The valleys are probably more hospitable for recolonisation through their higher salt content gained by this drainage. The acidity is always decreased by a fire and owing to the equalisation of texture becomes more similar at the 2-inch and 9-inch depths.

During recovery from burning there is a gradual increase in humus and acidity and lastly in salts. The increase in acidity is more rapid in the valleys, so that the bottoms of the slopes come again to be considerably more acid than the tops. A factor aiding the production of relatively high acidity in the valleys may be the reduction in the ameliorating drainage effects through the greater accumulation of humus.

A method is developed for the quantitative evaluation of the extent of leaching and drainage effects on slopes as shown by the changes in the ratio of salts to humus at different levels.

Laboratory experiments show that water and salts pass more readily through burnt than unburnt soils and that absorption of salts is diminished by burning. A greater loss by leaching and drainage would therefore be expected on burnt than on unburnt areas. This is found in practice.

The soil characteristics of special ecological zones such as areas dominated by *Erica tetralix*, *Ulex nanus*, *Pteris aquilina* and *Vaccinium* or in which *Molinia* or *Aira* (*Deschampsia*) *flexuosa* become prominent features are briefly discussed and can be gathered from Table XV.

The results for certain zones of poor vegetation, gravel and bare patches, and concerning the distribution of potassium and aluminium are also given in the text.

In conclusion my thanks are due to Professor Fritch, both for the facilities offered me and for his advice and criticism. I am also much indebted to Dr Salisbury, who has been occasionally troubled for the sake of his helpful suggestions, and to many of the advanced students of this Department, who have been of great assistance to me both in the laboratory and in the field. Lastly, many thanks are also due to Mr W. A. Glanville, formerly of the Engineering Department here, who has carried out a special survey of the Heath and prepared an accurate map of the paths and contours, a copy of which has been used in the preparation of Fig. 1.

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EPHARMONIC RESPONSE IN CERTAIN NEW ZEALAND SPECIES, AND ITS BEARING ON TAXONOMIC QUESTIONS

By H. H. ALLAN.

(*With twelve Figures in the Text.*)

A. INTRODUCTORY

The development of genetics and of ecology in recent times is reacting strongly on taxonomy, and will have a more and more profound influence as accurate knowledge of organisms in the field and in the experiment garden increases. The problems of variation and the delimitation of species are being viewed from new angles, and systematic work is becoming increasingly coloured by the new conceptions, while the effect upon evolutionary speculation is no less evident.

New Zealand floristic botany has been dominated by the conceptions of that *princeps botanicorum*, Sir J. D. Hooker, but admirable as are the floras produced under his inspiration it is becoming clear that a vast amount of intensive work lies before the taxonomists of the future, now that it is seen that variation cannot be accepted as a datum or put aside as a trifling matter, but must be analysed, as far as may be, according to its diverse causes. The dictum of Lotsy (**20**, p. 41), "inheritable variability does not exist," must be proved or disproved—it cannot be neglected. Hooker (**18**, p. viii), from his extensive knowledge of plants the world over, both wild and cultivated, living and stored in herbaria, was led to conceive of species as being widely spread and very variable. He says (*l.c.* p. xiii): "The result of my observations is, that differences of habit, colour, hairiness, and outline of leaves, and minute characters drawn from other organs than those of reproduction, are generally fallacious as specific marks, being attributable to external causes, and easily obliterated under cultivation. It has hence been my plan to group the individuals of a genus which I assume after careful examination to contain many species whose limits I cannot define, that the species shall have the same relative value as those have of allied genera whose specific characters are evident." As an illustration he takes *Blechnum capense* (*Lomaria procera*): "The resident may find two varieties of this and of many other plants, retaining their distinctive characters within his own range of observation (for that varieties often do so, and for a very uncertain period, both when wild and also in gardens, is notorious), and he may have to travel far beyond his

own island to find the link I have found, in the chain of forms that unites the most dissimilar states of *Lomaria procera*; but he can no more argue thence for the specific difference of these, than he can for a specific difference between the aboriginal of New Zealand and himself, because he may not find intermediate forms of his race on the spot" (*l.c.* p. xiv).

Following these lines of thought taxonomists dealing with New Zealand material have tended to unite groups which, however distinct their extreme members, are connected by a series of "intermediates," the species then being spoken of as "variable." Carried to its logical conclusion Hooker's view justifies the action of Mueller (**21**, cited in **4**, p. 446) in grouping together all the Australian and New Zealand, and most of the South American, gentians under the one name *Gentiana saxosa*! The fact that we may find a form in South America that is a "link" missing in a chain of forms in New Zealand does not seem to prove anything, unless we know the causes operating in the two countries to produce the intermediates. Whether we give the Maori and the various types of Europeans in New Zealand varietal or specific status matters little. Intermediate forms are common enough, and the reason for them is well enough known! The finding of a race having intermediate characteristics in, say, one of the Pacific Islands would be interesting, but would not explain away the half- and quarter-caste.

However far from complete our analysis is, we now know that intermediates fall into several distinct classes. We have: (1) Aggregate species made up of a number of distinct microspecies—the Linneons and Jordanons of Lotsy (*l.c.* p. 27)—that remain constant when self-fertilised; e.g. certain varieties of *Hebe salicifolia* (**11**, p. 200). Into the vexed question of their origin, whether mutational or what not, we need not here enter. (2) Groups in which the intermediates are apogamous races, whether their origin be by hybridisation or not, e.g. certain forms of *Erophila verna* (**22**, p. 11). (3) Groups of intermediates due to hybridisation. These groups may be (*a*) inconstant forms, not breeding true, e.g. × *Coprosma Cunninghamii* (**2**, p. 310), or (*b*) constant forms, breeding true[1]. (4) Groups of intermediates due to epharmonic response to environment. Possibly in certain cases such intermediates may ultimately become constant, or certain of the forms may, as suggested by Cockayne (**10**, p. 25) for *Edwardsia prostrata*. (5) Groups in which individual differences occur that cannot at present be assigned to any known cause. In general, e.g., the juvenile form of *Aristotelia fruticosa* can be correlated with its environment as epharmonic, but the wonderful minute differences in leaves on individual plants defy analysis (Fig. 1). It is easy but not enlightening to speak of them as "fluctuating," "spontaneous," and so forth. When *A. serrata* occurs in company with *A. fruticosa* forms of the hybrid × *A. Colensoi* will be met with, and the confusion becomes worse confounded.

[1] Such supposed "constant hybrids" need critical examination. The example of × *Geum intermedium*, alleged by **Blaringhem** (**3**, p. 322) to be constant, is said by **Weiss** and **Rosen** (*Nature*, 4th Oct. 1924, p. 500) to show distinct segregation of characters in F 2.

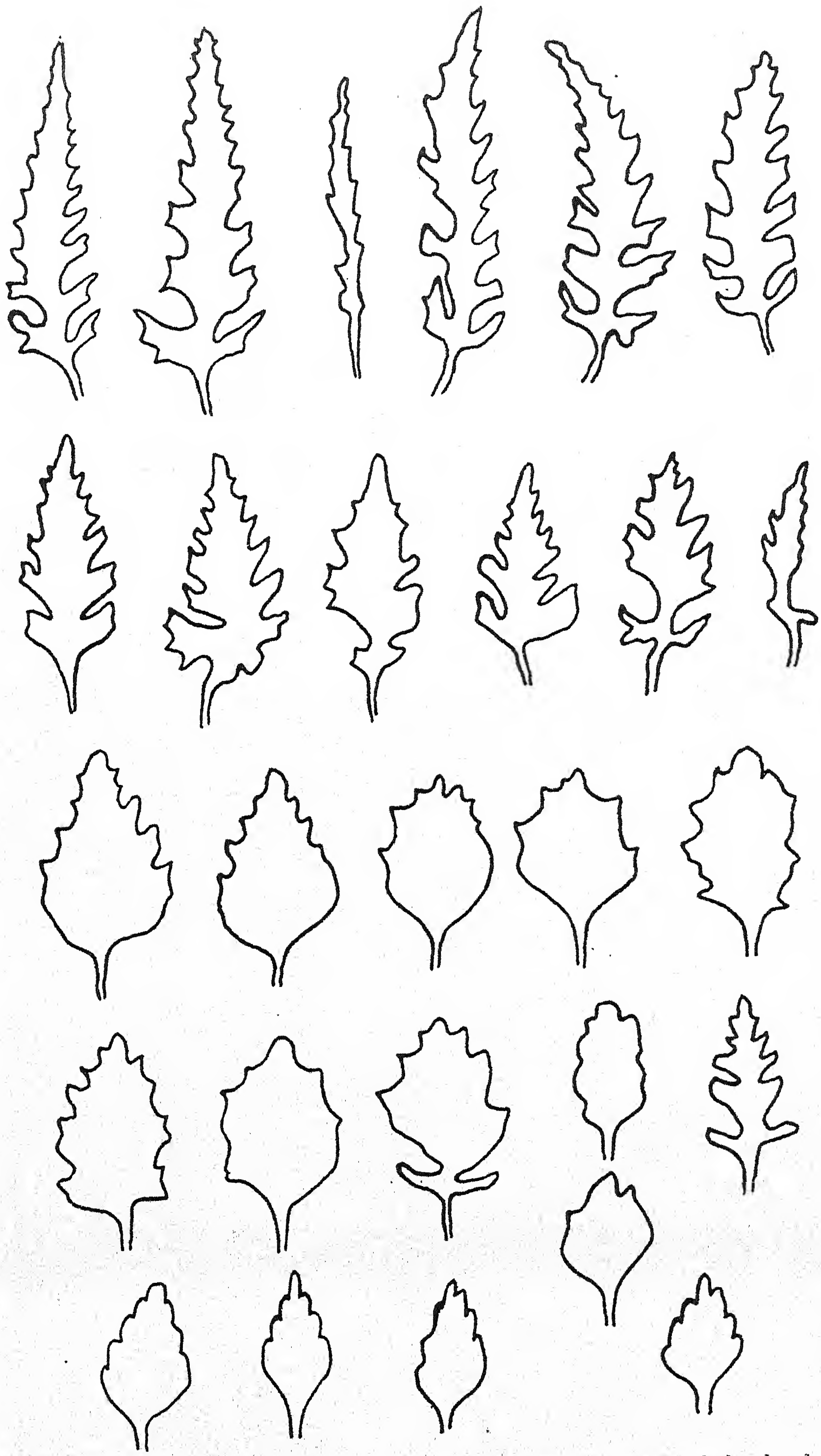

Fig. 1. Leaf-tracings of juvenile *Aristotelia fruticosa*. The leaves were irregularly placed on a single branch; forms on the lowest line approximate to those of the adult.

In nature these groups may be almost indissolubly entangled, but field studies supply many clues as to the most profitable lines of research in any particular examples of groups of intermediates met with, and it is no longer possible to rest content with a simple description of the polymorphy that exists, or with a statement that the species is very variable. And while Hooker's position as regards "links," and as to hybridisation (*l.c.* p. xv), is no longer tenable, it remains true that the essay of 1853 still repays careful reading.

Readers who wish to review the present state of our knowledge of these matters in the New Zealand flora, should consult Cockayne's important papers and books (**6–16**). It may, however, be well to indicate here the exact standpoint of Cockayne by citing certain of the principles laid down by him as a guide for the establishment of species or varieties (**13**, p. 161): "(1) The starting point in the setting-up of species is the individual. (2) Groups of individuals which resemble one another in every character and reproduce their like, subject, of course, to unfixed fluctuating variations, constitute specific units and may be designated 'microspecies.' (4) Two or more closely related microspecies may be united into a group for the sake of: (*a*) convenience in identification, (*b*) emphasizing the close relationship of minor groups (microspecies), (*c*) phytogeography. (5) Such a major group as constituted in (4) forms an aggregate or collective species. (15) In certain cases groups, otherwise well defined, seem to be united by 'intermediates' which cannot be joined to such groups or made into one or more species. Such 'intermediates,' according to the teachings of genetics, may be assumed to be hybrids between microspecies."

The following sections deal with certain examples of epharmonic response, roughly classified, that have come under my observation, and that bear on the questions raised in the introduction. The subject deserves extended study and would repay monographic treatment. I use the term epharmony to apply to all changes in the form of an organism traceable to varying conditions of the environment.

B. CHANGES IN LEAF SIZE, SHAPE AND TEXTURE

(a) *Ranunculus Monroi* var. *dentatus*. Kirk (**19**, p. 9) relies on the following leaf-differences in separating the variety: *R. Monroi*, leaves rounded reniform or nearly orbicular or ovate; crenate or crenate-dentate; glabrate or sometimes silky or villous—var. *dentatus*, leaves broadly ovate or ovate-lanceolate; crenate, lobed, or dentate; clothed on both surfaces with strigose ferruginous pubescence. Cheeseman (**4**, p. 12) accepts the variety, and only refrains from creating it a species owing to the "occurrence of numerous intermediates."

On Mt Peel, Canterbury, grows a plant referred to the variety, as a rock-plant from *c.* 950 m. upwards, descending along streams to much lower elevations. The changes in size and in the degree of tomentum on the leaves

is most striking, as shown in the following table. A complete series of inter-grading forms can be found according as the degrees of shelter, shade, root-room, and moisture change. Moreover I have produced similar changes in garden-grown specimens from the various habitats. Plants, also, taken from the rocks and replanted in a sheltered nook by a stream-side, grew in the course of two seasons into forms indistinguishable from those of plants growing naturally in the same spot. A plant intermediate between C and D of the table planted among the summit rocks grew into a form closely approximating to A.

Epharmony in *Ranunculus Monroi* Hook. f.

	Specimen from exposed rock-cleft *c.* 1300 m.	Specimen from sheltered rock-cleft *c.* 1300 m.	Specimen from stream-side *c.* 900 m.	Specimen from stream-side in shade *c.* 850 m.
	A	B	C	D
LEAVES	3–5 cm. by 2–3·5 cm.	5–8 cm. by 7–9 cm.	7–12 cm. by 7–10 cm.	10–13 cm. by 8–11 cm.
	Coriaceous, broadly ovate, crenate	Sub-coriaceous, broadly ovate, crenate	Rather fleshy to sub-membranous sub-rotund, cordate, crenate	Thin and membranous, similar to C, but larger and more irregular
	Tomentum extremely dense; below of shaggy appressed ferruginous hairs, above of long pale hairs	Tomentum similar to A but less dense and paler below, above scattered long pale hairs	Tomentum below much less dense; pale below, above of only scattered hairs	Tomentum reduced to very scant hairs below, glabrous above
PETIOLES	1–3 cm.	4–7 cm.	7–16 cm.	10–20 cm.
	Densely clothed with ferruginous hairs; sheathing-base 0·3–0·5 cm. by 1·5–2 cm.	Similar to A; sheathing-base 1–1·5 cm. by 2–2·5 cm.	Similar to A; sheathing-base 1–2·5 cm. by 3–5 cm.	Rather densely clothed with brownish hairs to glabrate; sheathing-base 2–3 cm. by 3–6 cm.
SCAPES	7–9 cm.	15–20 cm.	15–30 cm.	20–40 cm.
	Simple or once-branched tomentum dense, pale brown	Sparingly branched tomentum similar to A	Several times-branched tomentum less dense	Much-branched, sub-corymbose tomentum reduced to sparse pale hairs
BRACTS	0·5–1·5 cm.	1–3 cm.	3–4 cm.	5–6 cm.
	Linear to linear-lanceolate	Linear, lower slightly lobed	Lower deeply lobed	All except uppermost deeply lobed
SEPALS	6–8 mm.	7–12 mm.	10–13 mm.	10–15 mm.
	Dense pale-brown pubescence below	Pubescence hardly dense, still paler	Pubescence similar to B	Pubescence reduced to scant pale hairs
PETALS	9–12 mm.	9–12 mm.	10–15 mm.	10–15 mm.

It will be seen that as far as the Mt Peel plants are concerned Kirk's points of difference fall to the ground, unless by variety we merely mean an unstable form. This does not prevent the possibility of *R. Monroi* being an aggregate species, but proves that herbarium specimens alone cannot settle such questions (Figs. 2, 3).

Similar inter-grading forms were observed in the case of *Senecio bellidioides*, some answering to the description of var. *glabratus* (**19**, p. 339), but clearly related to their environment. Some subalpine forms of *Anisotome aromatica* are only distinguishable from *A. imbricata* by the characters of the fruit. The var. *incisa*, of the former species, distinguished by its flabellate or rhomboid leaves, is certainly a microspecies, but I have been able to alter its leaf-

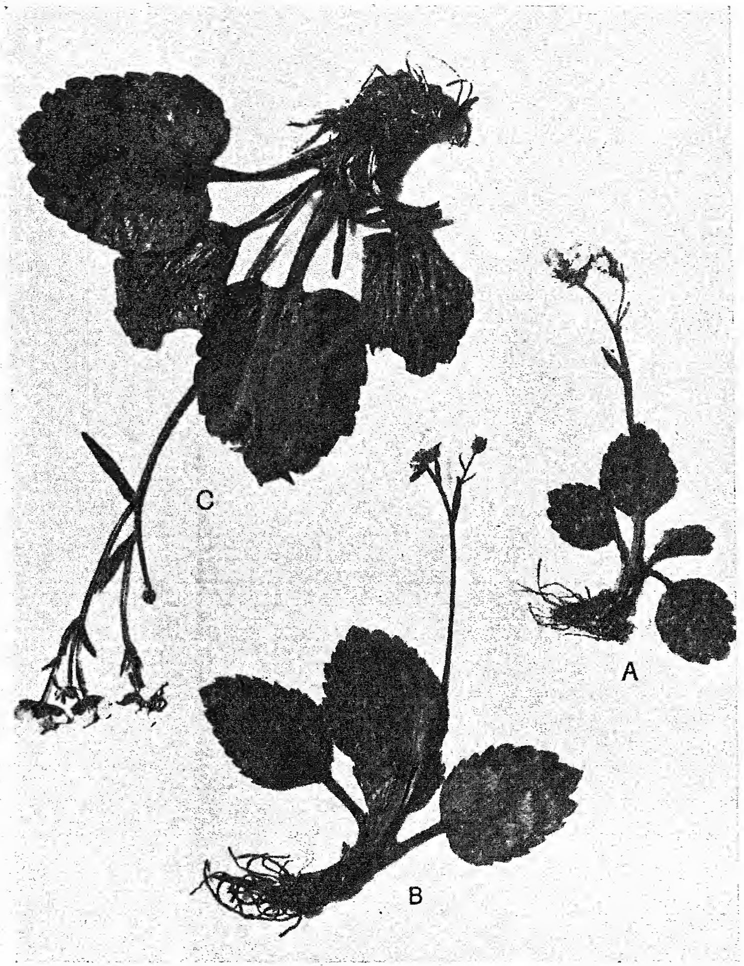

FIG. 2. *Ranunculus Monroi*, forms A, B, C of table.

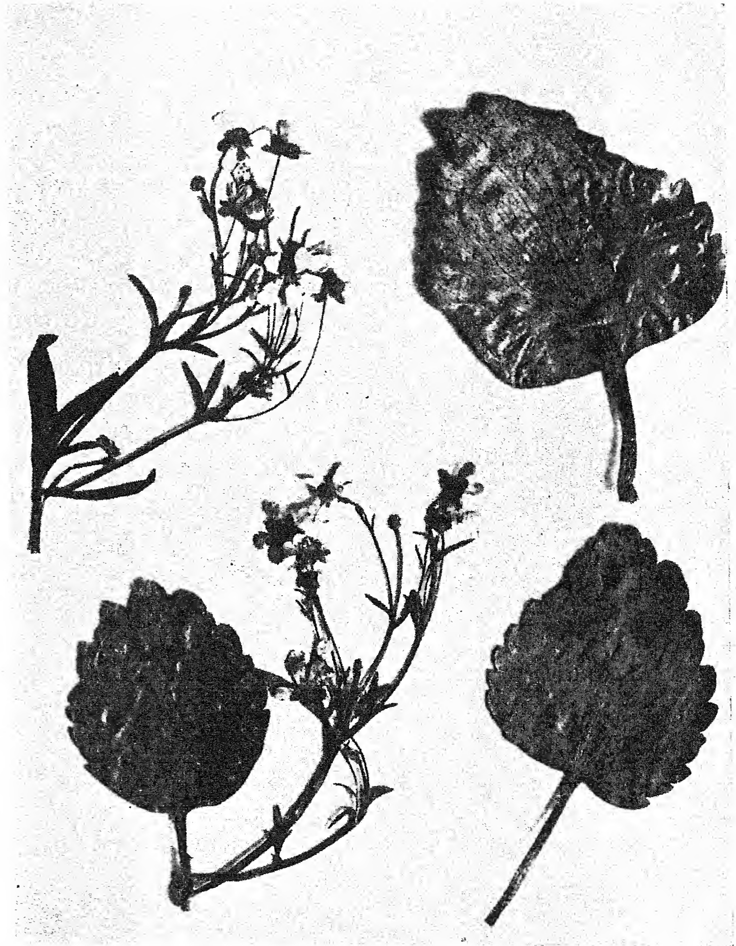

FIG. 3. *Ranunculus Monroi*, form D.

characters considerably in moist-air cultures (Fig. 4). Other examples of extremely plastic species could be given, and it seems wiser in such cases to use the non-committal term "form" till such time as research has differentiated the microspecies from the unfixed epharmonic forms.

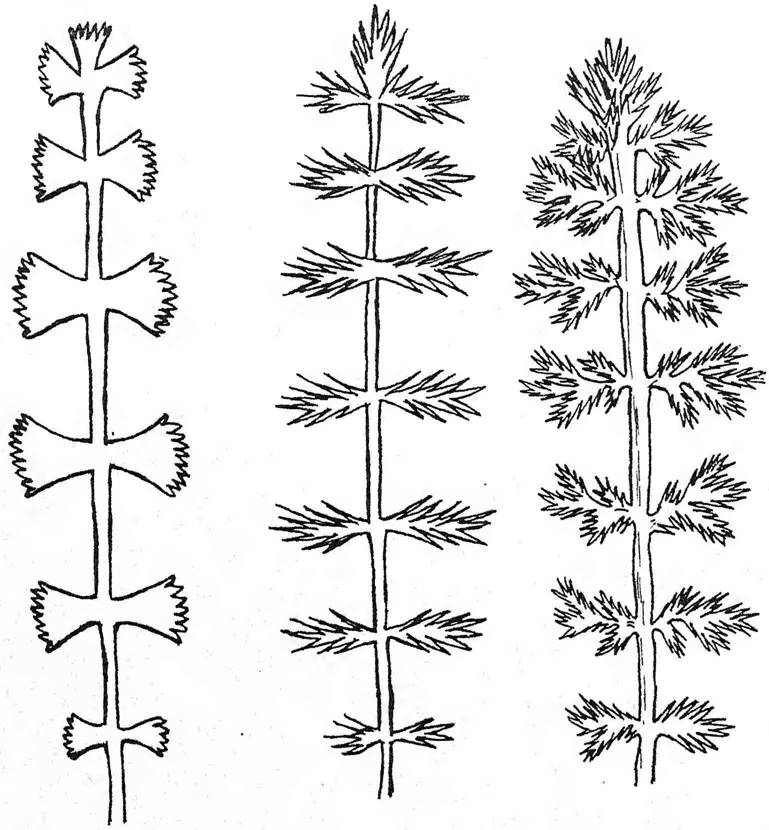

FIG. 4. Left—ordinary form of leaf of *Anisotome aromatica* var. *incisa*. Centre—leaf from same plant after cultivation in moist air. Right—leaf of typical *A. aromatica*. All ×3.

(b) *Plagianthus ribifolius*. A detailed account of the life-history of this species is given by Cockayne (**6**, p. 269). *P. Lyallii* has adult leaves ovate-acuminate, glabrous, with stellate pubescence on the mid-ribs and principal veins, while those of *P. ribifolius* are usually merely acute, and the stellate pubescence is not confined to the veins, the under-surface being covered with a dense mat of stellate hairs, the individual hairs longer than those of *P. Lyallii*. The distribution of the species is remarkable: *P. Lyallii* is apparently confined to regions of the South Island exposed to the great western rainfall; *P. ribifolius* occurs in the eastern mountain region, beyond the limit of western rainfall. Cockayne says (**6**, p. 272), "It is ecologically of extreme interest that a character seemingly so trivial as a slight variation in hairiness of leaf

has led to these two species not having intermingled, although they approach in places to within only three or four miles from one another at the most; and it shows, moreover, how an apparently unimportant character may govern the climatic distribution of a plant. It may also be pointed out that both forms thrive equally well side by side in lowland gardens where the rainfall is slight, and the characters of each, so far as I have been able to ascertain, remain unchanged."

Now *P. ribifolius* is a plentiful plant on Mt Peel, forming groves at elevations above the general forest line, and descending as occasional plants into the forest of the upper plains. The forest is true rain-forest, and the environment perfectly suited to *P. Lyallii*, but it does not occur. In dense shade by the sides of streams the Mt Peel plant, elsewhere typical *ribifolius*, becomes a shrub the leaves of which are almost identical with those of *P. Lyallii*, being much more acuminate, and having the pubescence practically confined to the veins. Rarely one finds specimens showing both forms of foliage. It would seem that research is required to determine whether we are not, after all, dealing with a species sufficiently plastic to adapt itself to the very different conditions of habitat in which the two forms grow. It may be that we have here an example of an epharmonic variation that has become fixed, or almost so, but the question as to the taxonomic status of the two forms seems still open.

(c) *Olearia capillaris.* This species is treated by both Kirk (**19**, p. 268) and Cheeseman (**4**, p. 285) as a variety of *Olearia arborescens*, the latter writer stating (**5**, p. 88): "the variety *capillaris*, although remarkably distinct in its extreme form, can be traced step by step into the ordinary state." As stated by Cockayne (**16**, p. 117) the "steps" are almost certainly due to hybridisation. *Olearia capillaris*, if that name be confined to the "extreme form," is a semi-divaricating shrub with leaves $\pm$ 7 mm. long, while *O. arborescens* is a bushy tree, with leaves $\pm$ 50 mm. long.

At the same time *O. capillaris* is remarkably responsive to environment. Whereas the adult has leaves 5–7 mm. by 6–8 mm., broadly ovate or suborbicular in outline, with sinuate margins, juvenile plants growing in dense forest shade are of open habit, sparingly branched, with much larger leaves, 18–30 mm. by 20–35 mm., having crenate-sinuate margins. The branches are often more or less prostrate and rooting. Where both parents occur, there will occur the hybrid forms, and the status of individual juveniles will become very difficult to determine. It is obvious that taxonomists have here a group that must be taken to the experiment garden to be discriminated (Fig. 5). Large-leaved juveniles growing in my garden are now producing leaves of adult size and form.

(d) *Olearia virgata.* This species has been described by both Kirk (**19**, p. 276) and Cheeseman (**5**, p. 19) as very variable, and several varieties have been created. It is undoubtedly a big and difficult aggregate group, one race

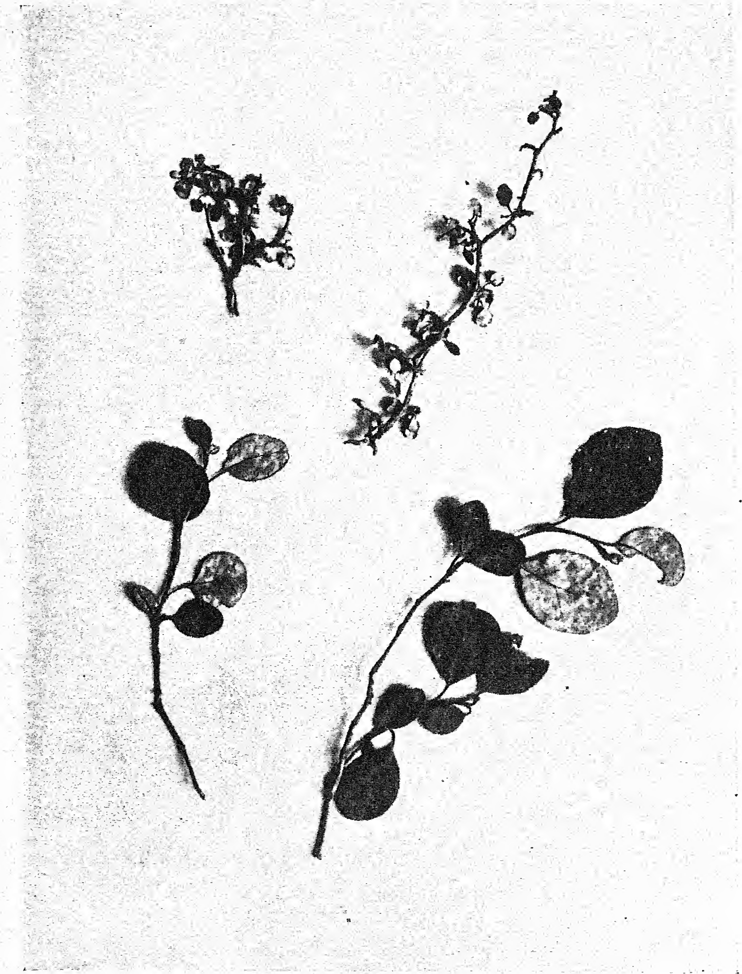

FIG. 5. Juvenile (lower) and adult (upper) forms of *Olearia capillaris.*

FIG. 6. (*a*) Normal and two reversion shoots of *Olearia virgata* var. (North Island). (*b*) Lower—grassland form of *Olearia virgata* var. (South Island). Upper—forest form of same var.

of which has been segregated by Cockayne (**9**, p. 173) as *O. lineata*, a course which field evidence strongly supports, and further segregations will certainly be made. Nevertheless certain forms are very plastic, and the epharmony of the aggregate requires investigation before an intensive treatment can be satisfactorily carried out.

In the rain-forest climate of Feilding, North Island, a very distinct-looking form grows as a forest-margin plant of rather densely divaricating habit. It is also prominent in certain swamps. The leaf-blade is coriaceous, quite flat, or the margins minutely recurved. The leaves are glabrate above, and clothed in dense, appressed tomentum below. They average 3 mm. by 6 mm., with petioles of 2 mm. One rather large specimen, growing under trees of *Leptospermum ericoides*, had been cut down and was regenerating from the base. The shoots were erect, sparingly branched, and the leaves thin and flat, averaging 8 mm. by 16 mm., with petioles up to 12 mm. The upper surfaces were glabrous, and the lower only thinly pubescent. A cutting from this has reverted in my garden in a single season to a widely divaricating form with leaves precisely similar to that of the ordinary form (Fig. 6, *a*).

C. IN-ROLLING AND FLATTENING OF LEAVES

(a) *Olearia virgata* var. A distinct microspecies from the one referred to above is common in the tussock-grassland and swamp at Mt Peel. It is a rather densely divaricating shrub with branchlets slender and clothed with dense white pubescence. The leaves have strongly recurved margins, so that they become linear and semi-terete in gross outline, resembling but much shorter than those of *O. lineata*. They are collected mainly in opposite fascicles on short arrested branchlets, are dark green above with many rather long soft hairs, and are densely covered below with white tomentum, among which are numerous scattered long hairs similar to those of the upper surface. The average measurements are 1·5 mm. by 7 mm., with petioles 2 mm. When forced flat the blades are 3 mm. wide.

Plants are occasionally met with growing in forest shade a little way from the margin. The effect of the environment is to give the plant so different an appearance that it was considered by a prominent New Zealand taxonomist to be an undescribed species, till specimens were obtained showing that it was another case of unfixed epharmonic response. The branches lose their divaricating habit, and the plant becomes a lax open shrub with scanty pubescence on the branchlets. The leaf-bearing branchlets lengthen out, separating the opposite pairs of leaves, which become perfectly flat and average 8 mm. by 17 mm., with petioles of 3 mm. The upper surfaces carry few or no hairs, the pubescence beneath becomes thinner, with only few scattered long hairs. The leaf-tip becomes minutely apiculate, instead of merely acute.

Specimens were found on the adjacent grassland showing every gradation of leaf-form and size. These plants were surrounded by a dense growth of

tussock-grasses and *Blechnum capense*. Shoots growing amidst the grass and fern had leaves identical with those of the forest form, and were succeeded above by a series becoming gradually smaller and more recurved as the branches reached above the surrounding vegetation, till the uppermost parts of the shrubs assumed the divaricating form of the open grassland. Plants of the latter form cultivated under shade changed into that of the forest (Fig. 6, *b*).

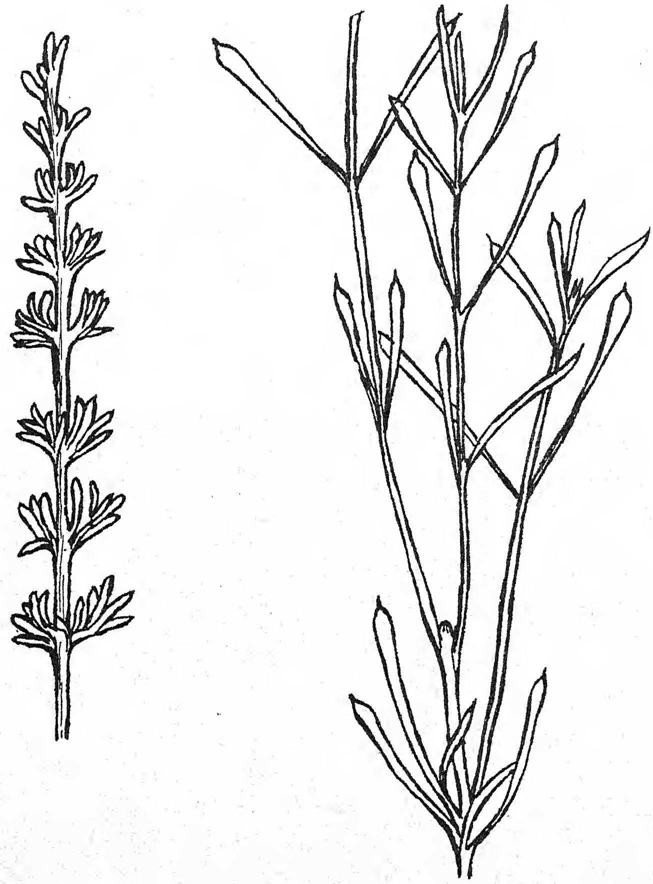

Fig. 7. Left—normal shoot of *Olearia Solandri*, ×2. Right—reversion shoot from same plant, nat. size.

(b) *Olearia Solandri*. This species, similar in many respects to *O. virgata* but of different habit, is marked by the golden tomentum of the branchlets. The tomentum of the under-surface of the leaves is also said to be pale yellow, but it is white in all specimens examined by me. This yellow tomentum is often very deep toned in seaside plants, but is paler on inland ones, and is also less viscid. The leaves are linear or linear obovate, with mid-ribs prominent below and much recurved margins. They average 5 mm. in length, including

the petiole. Plants growing in the shade of *Leptospermum* thickets have rather larger leaves, less recurved, and with thinner tomentum. The colour of the branchlets is very much paler. Reversion shoots may sometimes be found near the base. These are slender, erect, with thin white tomentum. The leaves are flat with very thin white tomentum below, and average 20–30 mm. in length (Fig. 7).

(c) *Paratrophis opaca.* This species was accepted by Cheeseman with considerable hesitation (**4**, p. 633) as intermediates exist between it and *P. microphylla*. The former has leaves ± 10 cm. long, the latter ± 2 cm.

FIG. 8. Normal and rolled-leaf forms of *Paratrophis* from the same plant.

and with a distinct juvenile small lobed-leaf form. The intermediates are almost certainly hybrids, but there is considerable reduction of size in leaves of *P. opaca* on trees growing in exposed situations. The form illustrated (Fig. 8) is probably a hybrid. Sheltered leaves are ± 3 cm., thin in texture, flat; leaves on the upper part of the shrub, exposed to salt gales, are of the same size, but more coriaceous, with the margins much recurved, often right to the mid-rib. They are also sub-erect on the branchlets, not spreading. I have observed only the one plant of this form showing leaves both flat and recurved, but in the same locality—Titahi Bay, west coast north of Wellington

—a similar recurving was noticed on specimens with leaves nearly approaching those of *P. opaca* in size.

In these cases the leaf-inrolling is unfixed, the plants responding directly to the changed conditions, but in the case of *Olearia nummularifolia* and *O. cymbifolia* it is possible that an originally epharmonic change has become fixed. The latter differs from the former in having much recurved leaf-margins, and is treated as a variety of *O. nummularifolia* by both Kirk (**19**, p. 273), who suggests that it "appears to be a depauperated condition, largely caused by the ravages of insects," and Cheeseman (**4**, p. 290), who speaks of its distribution as local.

Cockayne has been able (**14**, p. 72) to flatten the leaves in moist-air cultures. He also considers (**16**, p. 127) that hybrids between the two occur wild. Evidently further work is desirable on these two species.

D. THE ASSUMPTION OF THE LIANOID HABIT

(a) *Senecio sciadophilus*, a species occurring in a few scattered localities in the South Island, is of interest from the varieties of habit it assumes, though it raises no taxonomic difficulties. The following description is drawn up from observations at Mt Peel. The seedling has leaves spirally arranged, tri-lobed, or rarely tri-foliate, with the toothing of the edges less marked than in the adult. The slender stem may commence twining if situated near a slender support, but more commonly flexes over and grows along the ground, with ascending tip. The leaves then formed have the orbicular, coarsely toothed adult form, and the spiral arrangement becomes obscured by the twisting of the petioles. The stems branch freely, root at the nodes, and form a loose mat. The branches grow over logs or low shrubs in a tangled mass, or if the bush is taller ascend in a slightly twining manner and form a scrambling cover to the shrub. Long semi-erect shoots grow out, and, meeting a suitable support twine vigorously, or, failing support, incline over and are added to the general mass. Such shoots may even again reach the ground and take root. Short side shoots grow erect and bear the flowers. The twining is both sinistrorse and dextrorse, the former being more common, and these shoots may reach to the top of tall shrubs, there again to develop a scrambling mass of flexuous stems (Fig. 9).

(b) *Fuchsia Colensoi* is one of the "very variable" species of the floras. Much of the polymorphy can be traced to hybridisation with the tree, *Fuchsia excorticata*, but there are also probably distinct microspecies, and there may well be, as suggested by Cockayne (**10**, p. 21), climbing and non-climbing races. The form found at Feilding, which I have briefly described elsewhere (**1**, p. 403), is always a scrambling liane, there being no intermediates where *F. excorticata* is absent. The plant when growing in the open forms mounds of interlacing stems, thus agreeing exactly with the behaviour of species of *Rubi*,

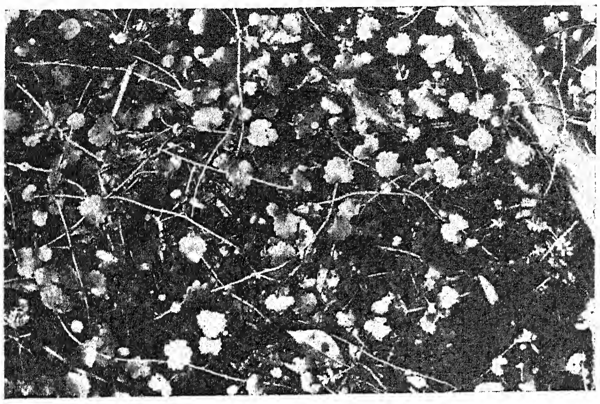

FIG. 9. The liane *Senecio sciadophilus* as a loose-mat-forming floor plant.

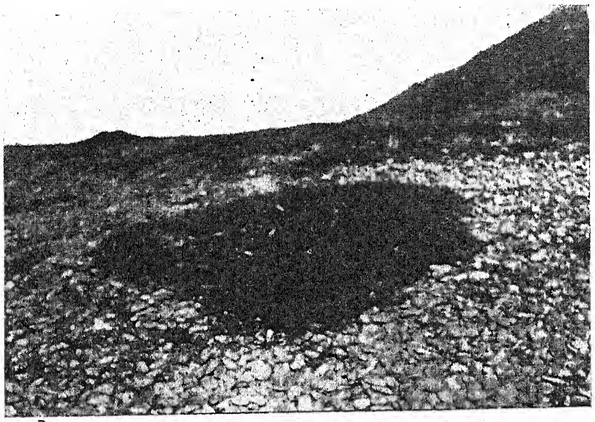

FIG. 10. Prostrate form of *Coprosma propinqua* var. on shingle beach.

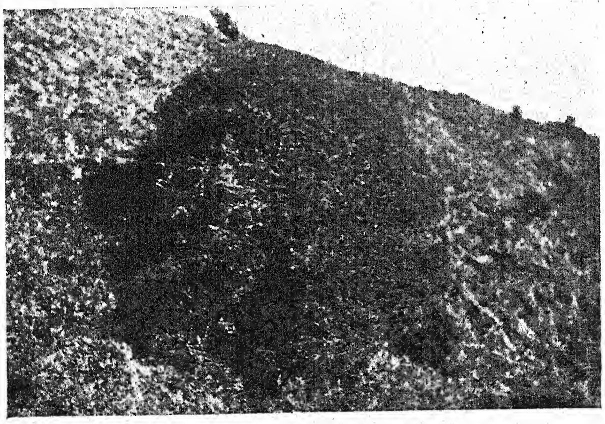

FIG. 11. Densely divaricating form of *Coprosma propinqua* var. on open hill-side.

as described by Cockayne (**10**, p. 22), and differing from the South Island twiggy shrub of the grasslands.

(c) Certain herbs. *Lobelia anceps* assumes a variety of forms consonant with its habitats. The salt meadow plant is usually suberect, rather stout, with rather large succulent leaves. Growing on banks and cliffs it becomes prostrate or drooping, and with suitable substrata the stems root freely at the nodes. Inland forms are more slender with thinner leaves. Growing under shrubs the plant may be met with as a small scrambling liane with weak slender stems up to 1 m. long and very sparingly branched. Field studies thus suggest that we have one very plastic species, and not a series of microspecies, but experimental study is required.

Stellaria parviflora. This is usually a small diffuse herb of the forest-floor, sometimes, however, forming dense matted patches. At the forest margin I have noted it assuming the lianoid form on shrubs and small trees. The ascending tips of the stems turn up through twigs and the internodes elongate. Slender side branches droop from these and help as supports, while short roots are given off at the nodes and may ensconce themselves in crevices and afford a firm support. The tallest example I have noted reached over 1 m. high, but usually it is much shorter.

Acaena Sanguisorbae. Several varieties of this aggregate are able to become small lianes. In its usual growth-form the species is a creeping and rooting semi-woody plant forming loose mats. In rain-forest climates the plants, when growing amongst small bushy shrubs, become lianoid, the tips of the stems growing up through the branches as searcher-shoots. On reaching the upper part of the bush these stems branch, scramble over the shrub, and may again incline downward and take root. Such stems are often $\pm$ 2 m. in length, with sometimes abortive roots at the nodes.

The case of the exotic grass *Agrostis tenuis* may be mentioned, its behaviour resembling that of *Acaena Sanguisorbae,* and occurring in similar situations. Sparingly branched stems over 2 m. long may be found growing over shrubs on the outskirts of forest.

E. THE CREEPING AND ROOTING HABIT

(a) *Myrtus pedunculata.* As pointed out by Cockayne (**8**, p. 19) *Myrtus pedunculata* and *Leucopogon fasciculatus* are examples of shrubs that have an erect bushy form, and also a prostrate one. In part such changes of form are unfixed epharmonic responses, but there are cases that are difficult to explain on this ground, and a critical study of the matter is much required. *M. pedunculata* is an aggregate species, there being very distinct varieties among the erect forms. It may well be that certain creeping forms are microspecific. In the Southern Beech forest of North-west Nelson there occur patches several square miles in area composed of the decumbent stems of *M. pedunculata,* connected below by far-spreading, branching, horizontal

rhizomes. From these develop miniature thickets of erect bushy stems, the decumbent stems dying away. With the growth of the erect stems, and the dying out of some, open patches of shrubs are formed that could easily be

FIG. 12. Normal and shade leaves of *Coprosma propinqua* var. from the same plant.

mistaken for individual plants were the sequence not studied. In other forests erect forms occur in which no trace of a creeping habit can be found.

Cyathodes acerosa, too, may form open mats, or dense bushes, the two

forms sometimes growing alongside one another. The phenomenon seems much rarer in this species than in either *M. pedunculata* or *L. fasciculatus*, so far as my observations go.

A case that is certainly unfixed epharmonic response is that of *Helichrysum glomeratum*. This is usually an erect bushy shrub, but in dense forest shade, an unusual station, I have met it as a decumbent shrub, the long trailing branches rooting freely where they touch the ground.

(b) *Coprosma propinqua* var. Cockayne (7, p. 378) has described the epharmonic response shown by *C. propinqua* as a coastal plant. "This shrub, in its usual stations, such as lowland or subalpine scrubs and fresh-water swamps, is erect with numerous more or less divaricating branches. But when it grows on the coast....it is usually much 'wind-shorn' and frequently quite prostrate, being flattened against the rocks which emerge from the peaty ground, and clinging closely to their surface. But all transitions may be seen, from the wind-swept plant to the normal, and there is no reason to expect that the former form is in any way hereditary." I have been able to study these changes in a variety of *C. propinqua* growing on Kapiti Island. The prostrate form grows on the large shingle banks of the coast, and the stems do not strike root. Probably the insolation has much to do with the growth-form. On the lee sides of the shingle banks the plants are less prostrate, and on the forest margin are of ordinary divaricating form. Growing in the shade the plant becomes open with much larger leaves (Figs. 10, 11, 12). Cockayne, however, has shown (7, p. 379) that the prostrate form of the species growing on Chatham Island retains its habit even under cultivation in sheltered positions, and considers that there is here evidence as to fixation of acquired characters.

(c) *Hierochloe redolens*. The segregation of the microspecies of this aggregate is complicated by the presence of epharmonic forms. The following growth-forms were noted at Mt Peel. In the tussock-grassland the species is generally a robust semi-tussock grass, but when growing on the trunks of *Carex secta* in swamps, it is reduced to loose tufts. On steep moss-covered banks over which water trickles it is a tuft-plant with long flaccid drooping leaves. In the stretches of *Blechnum capense* on the open hill-side there is a form with well-developed rhizomes, the plant covering considerable patches.

F. FLOWERING JUVENILE FORM

Of the 200 or more species of New Zealand plants that have a juvenile stage very distinct from the adult, a certain number have been observed to flower both on the adult and on the persistent juvenile base, or on reversion shoots of juvenile form. *Dracophyllum longifolium* was observed by me to flower while still in the juvenile form. The differences between the juvenile with its long, spreading leaves, arching downward, and the adult with smaller, narrower, stiff, erect leaves, are very pronounced. Plants that invade the

upper forest margin from the lower subalpine shrublands at Mt Peel retain the juvenile form of leaf for long periods. The growth-form is no longer fastigiate, the plant becoming a shrub about 2 m. tall, with spreading naked branches, ending in rosettes of leaves of the juvenile form. In this condition the plant flowers and fruits freely. A taxonomist dealing with the two flowering forms, and not knowing the life-history of the plant, would certainly consider them two distinct species. *Pennantia corymbosa* also flowers while still in the juvenile stage, apparently rarely, though specimens flowering on the persistent juvenile base and on the adult portion are more commonly met with.

G. COLOURATION PHENOMENA

Very little work has been done in New Zealand on colouration as affected by environmental conditions, but although we have little suggestion of the beautiful autumn colouration of other lands there is much interesting material awaiting study by the ecologist and physiologist. Here a few points germane to this paper are noted.

(a) *Azolla rubra.* Plants of this species growing in shade have the leaves a beautiful sage-green. Such plants brought into the light rapidly turn the usual reddish colour. A number of other species could be cited showing similar epharmonic colour reactions, e.g. the bronzing of leaves of *Rubus subpauperatus* in winter, the purple colouration of *Agrostis subulata* in exposed subalpine stations. Not the least striking is the purple form of the exotic *Cerastium vulgatum* in fell-field.

(b) *Schoenus pauciflorus.* Growing in the sun-exposed swamp or bog this species has erect reddish stems, and when dominant forms conspicuous patches. It is also to be found along stream-beds and on wet rocks, where, if in shade, the stems are a deep green and often of a drooping habit. This change may be easily induced by transplanting. But, rarely, in the swamp one meets with plants devoid of the red colouration, growing alongside those of the usual hue. A study of these may show that there are two distinct varieties with constant colour differences, one permanently green, the other able to assume the red colour.

An analogous case is that of *Epilobium melanocaulon,* a plant of debris slopes on the high mountains, where forms with the "typical" blackish stem and dark red leaves may be found growing alongside others with greenish stems and gray-green leaves. There is little doubt that these forms are constant varieties, but a physiological examination of the plants should give valuable results.

(c) *Coprosma brunnea* and *C. acerosa* are two closely allied species differing, among other things, in their colour. The former, an inland plant of dry stony situations, has dark brown leaves and stems, the latter, confined to the coastline, has yellowish stems and yellow-green leaves. Leaves in the interior of

the bush, in both species, are sometimes quite green. These species illustrate excellently the futility of relying upon herbarium specimens alone in drawing up diagnoses and deciding specific status, dried specimens having much the same colour in each case, and other differences being obscured. A fuller consideration of these forms is to be published elsewhere. It would seem well worth while to grow each in the station of the other.

(d) *Geum parviflorum* usually has green leaves. Specimens gathered by me high up in subalpine herb-field had deep-bronze coloured leaves. These plants cultivated in the lowlands retained their colouration for two seasons, and then gradually assumed the usual green tint. This experience suggests both that epharmonic responses may tend to fix themselves, and that one should not too hastily assume that any particular character is permanent.

H. CONCLUSION

These examples of epharmonic response in plants, together with those recorded in the literature cited, and with others that are accumulating, afford evidence that the taxonomist dealing intensively with species has a most difficult task, and that he must base his decisions regarding critical forms not solely upon herbarium specimens, but must take field and experimental studies into consideration, and bear in mind all the lines of work indicated in the introduction. In this critical taxonomy the phenomena of epharmony take a prominent place. It is the merit of the ecological outlook that it reinforces all branches of botany, freshens their outlook, raises new problems, helps the specialists to get a vista of the science as a whole, and provides a basis for the synthesis of their results. While Hooker's remarks as to the effect of cultivation in changing the form of plants are eminently true, the same responsive changes to environment are found in wild plants, and must be reckoned with. It is evident that so far from the flora of New Zealand being well known we are only at the beginnings. The labours of the past have furnished us with the rough working knowledge on which to build the finished structure.

Du Rietz (**17**, p. 112) has said, "Eine sehr produktive pflanzensoziologische Schule ist auf Neu-Seeland von L. Cockayne gegründet worden," and, as a humble member of that school I may here be permitted to pay tribute to my friend and master the founder, who has given me unstinted help and critical encouragement since, under his inspiration, I took up the study of botany.

Figures 2, 3, 5, 6, 12 from photographs by B. Hobday.

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CHARACTER AND CONDITIONS OF LIFE OF MARINE PHYTOPLANKTON

By BLODWEN LLOYD.

(*With five Figures in the Text.*)

CONTENTS.

I. INTRODUCTORY

Those free-floating unicellular plant organisms grouped collectively as phytoplankton comprise a plant-community as well-marked as those of terrestrial macrophytes. However, although plankton species have been recorded as early as the latter part of the eighteenth century[1], their evaluation as a distinct ecological unit dates from comparatively recent years.

This intensive study has been of later years largely a response to a growing realisation of their importance in the economy of the sea. Here, as on land, the synthesis of the carbohydrates and proteins necessary for animal nutrition is confined to the green plant organisms, which are thus the ultimate source of such organised foods. The whole varied range of animal life is therefore dependent on the two plant-associations found in the sea, namely: (i) the littoral forms, consisting largely of fixed macrophytic algae with also a small proportion of creeping benthic forms, and (ii) the phytoplankton. Now although the former may support a rich fauna locally, their activities are restricted to a comparatively narrow zone fringing the seas, whereas the latter are almost ubiquitous. It follows then that the phytoplankton is the more important unit in considering the organisation of complex food-materials from simple inorganic substances in the sea.

II. CHIEF ORGANISMS OF THE PHYTOPLANKTON

Among the phytoplankton, somatic organisation has not proceeded beyond the stage of the single cell as the complete individual. Within such a "somatella" (7), however, we may have a high degree of specialisation for locomo-

[1] *Biddulphia* (*Conferva*) *biddulphiana*, described by Smith, 1762. *Ceratium* (*Cercaria*) *tripos*, described by O. F. Müller, 1781.

tion, flotation, nutrition. Even where a social habit is adopted for better flotation, each cell retains its physiological independence.

Of those species which have succeeded in maintaining an existence in the free-floating habitat, by far the greater number belong to the Diatomaceae or the Dinoflagellata. The former are the more abundant in North temperate and polar seas, particularly in spring and autumn, while the latter abound in warmer regions.

(i) *Diatoms.*

The plankton diatoms exhibit great variety of forms, most of which are variants of the centric type, and are symmetrical either radially or about a median plane. *Coscinodiscus*, one of the simplest and commonest species, is almost drum-like in shape, the numerous discoid chloroplasts lying along the inside of the frustule-wall, and the nucleus being suspended in the centre by a densely granular protoplasmic bridge. This genus consists in all of some 45 species, including some of the largest diatom species (Fig. 1 i).

Several other common species are developmental forms from the *Coscinodiscus*-type; in *Thalassiosira* the frustules are connected by a single mucilaginous thread (Fig. 1 j), and in *Coscinosira* by several, secreted at adjacent valve faces. Other diatoms with circular regular valve view are: *Paralia*, where the frustules are strongly striate and adherent in long filaments; *Bacteriastrum* (Fig. 1 k) and *Corethron*, characterised by a ring of radiate setae around each valve; and *Stephanopyxis*, another filamentous form, bearing a corona of protuberances at the apex of each valve (Fig. 2 c).

Chaetoceras is a very varied genus of over a hundred species. The principal feature is the development on each valve face of a pair of hollow outwardly curved setae. These usually interlock with those of the neighbouring frustule, the terminal setae of a chain often being markedly distinct from the others. There does not, however, appear to be any plasmatic connection between the frustules. *Chaetoceras* is the only important genus which exhibits to a marked degree the social habit, but it seems thus to be well-adapted for flotation in the topmost water layers. Other forms also found floating in the upper surface waters are the numerous species of *Rhizosolenia*. These have an especially prominent girdle view, due to the intercalation between the valves of a number of plates. These may be almost circular, giving the frustule an annular appearance (e.g. *Rhizosolenia stolterfothi*, Fig. 2 a), or they may be rhomboidal in shape with a resulting imbricate effect (*Rh. shrubsolei*, Fig. 1 d and e).

Another numerically important diatom is *Biddulphia* with wide girdle view. The valves are either bilaterally compressed, or 3–4-angled, and possess a more or less pronounced protuberance at each angle. The euplanktonic species have in addition a pair of spines, which are not hollow as those of *Chaetoceras*.

The above are the more prominent diatom members of the phytoplankton, though in addition there are a number of species of the pennate type. These,

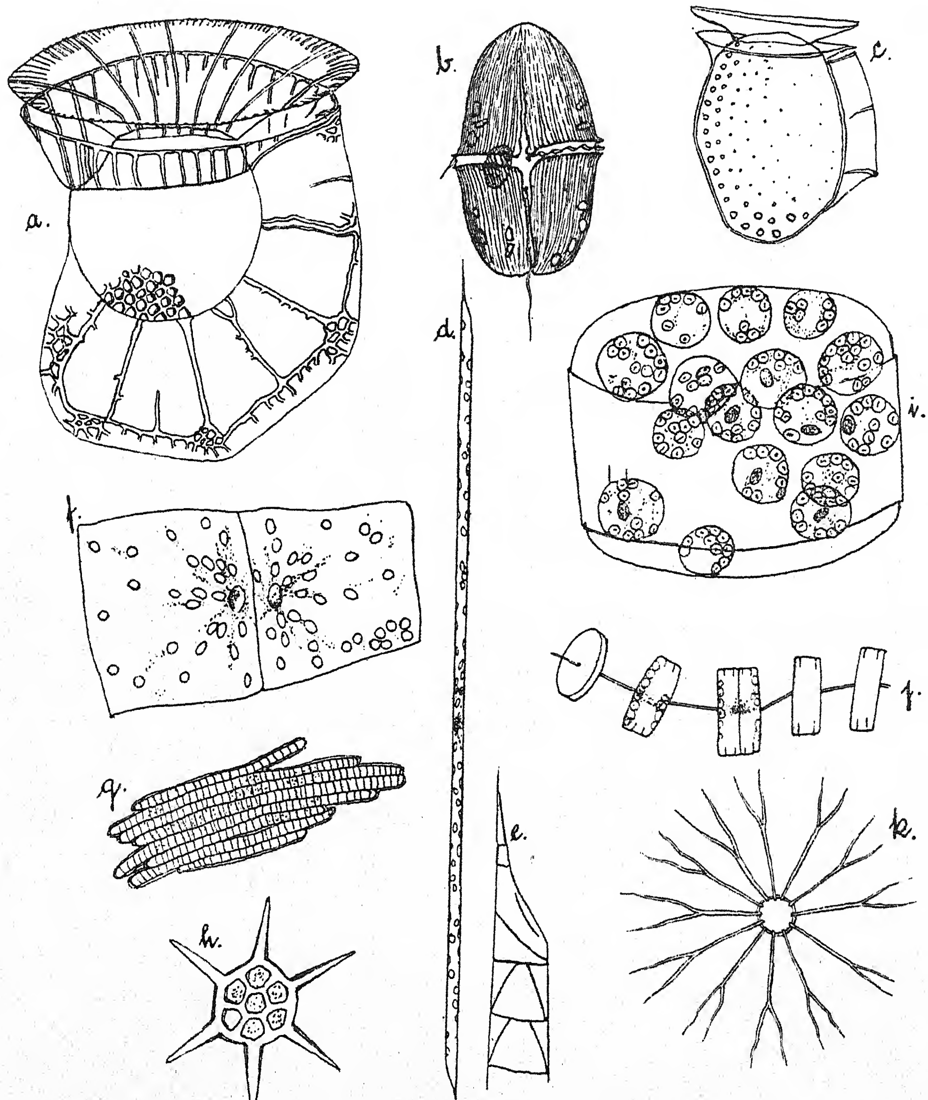

FIG. 1. *a. Ornithocercus steini* Schütt. ×400. Bay of Naples, 17. viii. 25. *b. Gymnodinium diploconus* Schütt. ×400. Bay of Naples, 25. viii. 25. *c. Dinophysis acuta* Ehr. ×400. Plymouth, v. 24. *d. Rhizosolenia shrubsolei* Cleve. *e. Rhizosolenia shrubsolei.* ×1000. *f. Streptotheca thamensis* Shrubsole. ×400. *g. Trichodesmium erythraeum* Ehr. ×200. From Brazil. *h. Distephanus speculum* (Ehr.) Haeckel. ×400. *i. Coscinodiscus concinnus* Wm. Smith. ×100. *j. Thalassiosira gravida* Cleve. ×200. *k. Bacteriastrum varians* Lander. Valve view. ×200.

Camera lucida sketches of specimens taken off the Welsh coasts, except where otherwise stated.

however, although they may be locally abundant in such numbers as to be the dominant form at any given time, do not exhibit such well-marked periodic habit or flotation devices as the true plankton species. Examples of such forms are *Nitzschia closterium*, *N. seriata*, and *Bacillaria paradoxa*. The significance of their occurrence in the plankton is dealt with in Section V.

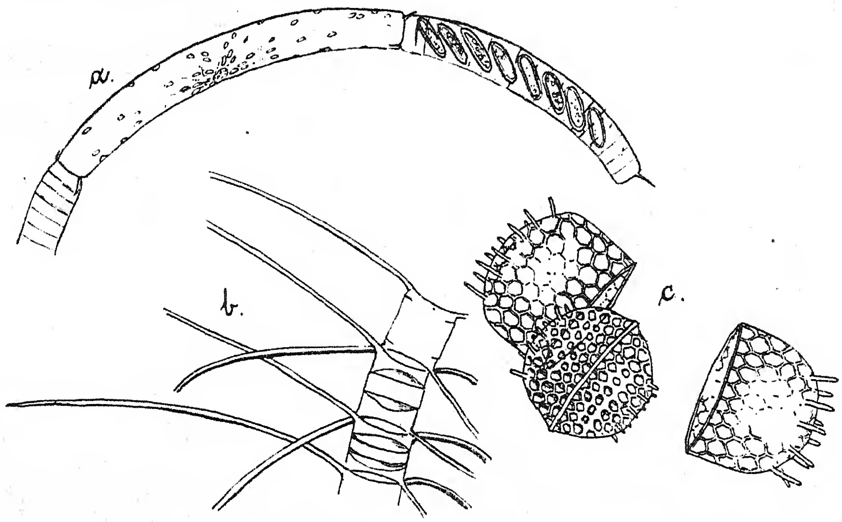

FIG. 2. Resting-spores of plankton-diatoms. All × 400. *a. Rhizosolenia stolterfothi* Perag. Off Aberystwyth. *b. Chaetoceras curvisetum* Cleve. *c. Stephanopyxis turris.* Off Saundersfoot, Pembrokeshire.

(ii) *Dinoflagellata.*

The Dinoflagellata are numerically inferior to the Diatomaceae of the seas, though "in abundance they are second only to the diatoms in the marine plankton, while locally and in midsummer they may far outnumber even these abundant organisms" (7). The particular biologic interest of this group lies in the fact that within the limits of a single genus, for example, *Gymnodinium*, we have methods of nutrition ranging from the purely holophytic to the completely holozoic.

Each of the two subdivisions, namely the Diniferidae with a girdle, and the Adiniferidae without a girdle, contains two parallel groups: (i) those protected by an articulated exoskeleton or theca and (ii) naked forms. Of those species present in the tow-net catches, the thecate forms with a girdle appear to be far more common than the other Dinoflagellata, mainly on account of their greater size, but also because the naked species are easily injured, and are especially susceptible to the changes in their environment consequent upon their capture and transfer to the laboratory.

Of the thecate Diniferidae, the genera *Ceratium* and *Peridinium* are the commonest in North European waters. Here they typically attain a maximal development in the summer months, and both individuals and species are

much more numerous in warmer waters. The presence of the covering theca increases the tendency on the part of the organism to sink; this is compensated for in the less robust and smaller forms by rapid flagellar activity, while in the larger and less mobile, spines and "fins" are often extensively developed, particularly in the tropical and sub-tropical species (Fig. 1 a and c).

Although the thecate forms exhibit great diversity of external structure, it is in the Athecatoideae that we find a greater range of plasmatic specialisation. On the whole, those forms with chromatophores are the more conservative as regards somatic specialisation within the single cell, but in the non-green species we find a range of "organelles" comparable to, and even highly resembling, analogous organs in the Metazoa. Kofoid states that these unarmoured forms reach their optimal development in eupelagic habitats. Certain species, however, are typically neritic, notably those arenicolous forms which colonise intertidal zones in such numbers as to appear to the eye as a discolouration of the sands.

(iii) *Protophyta cetera.*

Apart from the diatoms and the dinoflagellates, there are only a few species which occur in the phytoplankton in any large numbers. Of the Cyanophyceae, *Trichodesmium erythraeum* (Fig. 1 g) may be developed in extraordinary abundance in the warm seas. *Phaeocystis* spp. and *Halosphaera viridis*, brown and green algae respectively which may at any one time become the dominant form, occur in the summer months.

There are also a host of protist forms, some of uncertain systematic position, which occur in small numbers in almost any plankton catch, for example, the silicoflagellate *Distephanus* (Fig. 1 h), or, at a greater distance from land, the calcareous *Coccolithophora*.

III. BIOLOGY OF THE PHYTOPLANKTON

(i) *Periodicity and other Seasonal Changes.*

Variation in external conditions induces variation in the composition of the phytoplankton. Perhaps it would be more accurate to state that with a change in external factors there are concomitant changes in the plankton. The most striking of these is of course the apparent disappearance of some species at certain seasons of the year.

For the diatoms, which in the North temperate zone comprise at most seasons the greater part of the phytoplankton, the periods of maximal development are at about March and September. The absence of most diatoms during the unfavourable period may be accounted for in two ways: (i) that most forms of a given species die out, but leave a few hardy survivors which ensure the continuity of the species, or (ii) that some kind of resting stage is resorted to. The latter is the more reasonable assumption, but at the same time it is

a curious fact that such resting spores are only infrequent, and have not been described for all the known species by any means.

In *Chaetoceras* the highly characteristic resting-spores or "Dauersporen" are formed by the aggregation of the cytoplasm near the girdle-plane and by its subsequent encystment (Fig. 2 b). These spores may bear spinous outgrowths on one or both valve faces. The spore of *Stephanopyxis* resembles the parent frustule except for its smaller size and more robust areolation (Fig. 2 c). In *Ditylium* also only one spore is usually formed.

In the genera *Biddulphia* and *Coscinodiscus* the contents divide to form 2–64 nucleated sporules, each with chloroplasts, and a limiting cell-wall (Fig. 1 i). Bergon[1] records motile sporules in the former. A similar phenomenon was once observed by the writer in *Rhizosolenia shrubsolei*, where the cell-contents were divided into eight oval bodies arranged obliquely in the parent frustule (Fig. 2 a).

These spores do not seem to be equipped with any specific adaptation for resisting a rigorous period, so it is reasonable to suppose that they pass the resting period within the parent-cell. Nevertheless, it is remarkable that stages in such spore formation are not more common, particularly at the end of the period of maximal development for any given species. It is stated that these forms sink to their resting level before accomplishing this last act, the sinking being accomplished either by assimilation of the specifically lighter substances such as fats, contained in the cell, or in the bilaterally symmetrical forms by self-orientation upon a different axis, thus offering less resistance to the surrounding medium.

There yet remain to be considered changes in form other than resting stages. The most striking variation is that of size; in certain species, for example *Chaetoceras debile*, summer and winter forms differ so widely that they appear to be distinct species. Other changes in size, however, are not so evidently concurrent with varying external conditions. For instance, the larger, curved forms and smaller straight types of the diatom *Thalassiothrix nitzschioides* were easily distinguished, but no one type appeared to be restricted to any season. Such variations may be due to increased size after auxospore-formation, or possibly to the existence of genetically distinct strains within the limits of the single species.

(ii) *Reproduction.*

Mangin considers plankton diatoms as falling into two groups: (*a*) those which undergo a period of repose in some form or other, after which period they again begin active cell-division, and (*b*) dimorphic species with some individuals purely vegetative, and, later, others purely reproductive, only forming endocysts.

It has already been stated that resting stages are found comparatively

[1] **P. Bergon.** "Nouvelles recherches sur un mode de sporulation observé chez *Biddulphia mobiliensis* Bailey." *Travaux de la Station Zoologique d'Arcachon*, **5**, 1902.

infrequently; these are formed asexually. Sexual reproduction, as described for many benthic diatoms, has also been described in the plankton-diatom, *Corethron*, by Karsten[1].

Reproduction then in these unicellular forms is mainly a matter of somatic fission, and in both diatoms and dinoflagellates evidences of ordinary cell-division were naturally of frequent occurrence.

With regard to the diatoms of the plankton, the cell-wall is in most cases only slightly silicified, so that successive divisions do not necessarily imply progressive diminution in the size of the frustules, as in the case of the more rigidly silicified phytobenthon forms. Division of the nucleus is accompanied by infolding of the cytoplasm, the outer layers of which secrete a pair of adjacent valves in the ordinary way. This process is best seen in the larger forms, such as *Biddulphia regia*. Such daughter-cells may remain attached as a short chain, especially when divisions take place in quick succession. Where the adult form normally occurs as a chain the younger cells are often distinguished by the less marked thickening of the walls, and, in the spinous species, by the possession of less robust setae.

In the course of the writer's work on the phytoplankton of the Welsh coasts (**8**), efforts to obtain stages in nuclear division met with little success, although material was fixed under a variety of conditions and at all hours. No karyokinetic figures were found, and no stages intermediate between the elongated form of the resting nucleus with one or several nucleoli, and the two daughter-nuclei, each with one nucleolus. This may be due to the possibility that division takes place in a plane parallel to the greatest thickness of the cell, and it is difficult to focus high-power lenses through such a bulk of protoplasm. Again, embedding in paraffin and subsequent microtoming gave only distorted forms, due to the tearing of the cell-walls.

Although in the benthic diatoms a simple form of karyokinesis with numerous chromosomes takes place, it is conceivable that division in the more archaic plankton forms is of a much simpler order. Virieux[2] describes in *Coscinodiscus grani* a karyosomatic type of division; he states that the two nuclei resulting from the fission are each surrounded by a clear perinuclear tract. These zones are connected by a plasmatic bridge which appears to contain chromatinic elements.

In the Dinoflagellata the extra-nuclear cytoplasm is not concerned in cell-division. Nuclear division is karyokinetic, and even in the resting stage the chromatinic thread is distinct; this moniliform structure is characteristic of the dinoflagellates and serves to distinguish encysted stages, which often assume a form very different from the vegetative form.

Cell-division is oblique here. In the thecate forms, as in the diatoms, one part of the exoskeleton goes to each of the daughter-cells, the older half being

[1] **Karsten.** *Zeitschr. für Bot.* **4**, 1912.

[2] **J. Virieux.** "Structure et division cellulaire chez *Coscinodiscus grani.*" *Bull. biol. de la France et de la Belgique*, **64**, 1920.

often distinguishable by the more robust reticulations. Where any such thecate individual fails to divide, there is consequent over-thickening of the theca, with impeding of flagellar mobility. This results in phenomena of rejuvenation, which Kofoid considers as falling into groups: (i) cytecdysis, or shedding of the exoskeleton in pieces of a single or several plates, with ultimate renewal of the whole theca; (ii) cytexuviation, where the whole of the contents is extruded bodily from the theca (**7**).

(iii) *Nutrition.*

"Morphological distinctions, it has been said, are ultimately physiological ones" (**6**), and nowhere is this more evident than among the phytoplankton, in which are incorporated the very beginnings of the plant-habit. With the assumption of the chlorophyll-habit, there arises a two-fold necessity, as Church has pointed out (**3**), for development of a maximum surface for light-absorption, and also for "movements of translation at a rate different from that of the surrounding medium, whether faster or slower." He states further that such fast movement may be accomplished by flagellar activity, but that the nutritive effect may be increased quite as readily by any modification "involving a drag on the surrounding medium." The euplanktonic diatoms, though conceivably descendants of flagellated ancestors, are now non-motile, and are for the most part equipped with spines or protuberances capable of effecting the required "drag." The dinoflagellata, on the other hand, have except in the encysted stage retained the flagellate-habit. Now rapid flagellar activity makes higher demands on the available energy of the organism than the development of mechanical devices such as spines for resisting the tendency to sink. It may therefore be a significant fact that it is some members of this group that have lost the holophytic mode of life—none of the planktonic diatoms, on the other hand, are heterotrophic.

As to the actual food of the diatoms and the autotrophic dinoflagellata, since they are surrounded by their nutritive medium, there is never any problem of insufficiency of water and the commoner salts. At the same time, by the operation of Liebig's Law of the Minimum, any variation in those necessary substances present in minimal quantity will naturally affect the abundance of plankton forms. "The carbonic acid and the mineral salts are present in relatively large amounts, but the proportions of nitrogen compounds, silica and phosphoric acid in the water of the sea are very small....It is probable that the abundance of nitrogen compounds in the sea determines the production" (**6**). Evidence of this is given by Pearsall (**9**), who shows that diatom maxima are coincident with, and presumably affected by, spring and autumn river floods, which carry seawards an increased amount of soluble terrestrial compounds, including nitrates and phosphates.

By virtue of their ability to build these simple substances into complex organic compounds, the phytoplankton forms act as the "producers" of food

in the sea. All other non-green living forms, both plants and animals, which utilise these organised substances, are the "consumers."

IV. EXTERNAL CONDITIONS

The constituent species of the phytoplankton exhibit a striking seasonal development, like that of terrestrial plants: the direct causes of this periodicity are equally hypothetical. Herdman (**5**) ascribes such periodicity in marine plankton organisms to any or all of the three following causes:

(i) Sequence and periodicity of stages in the life-history of the organisms.
(ii) Irregularities due to the interaction of the organisms.
(iii) Periodic changes in the weather, composition of the sea-water, etc.

The two latter are more easily considered than the former, for, "in spite of the incredible amount of investigation that has been lavished on the speciography of this group, much remains to be discovered with regard to the reproduction and life-processes" (**6**).

The consensus of opinion is that such seasonal changes in the plankton associations are at least a reaction to, if not a direct result of, the stimulus of external conditions, though there is great diversity of thought as to which particular factor or group of factors is mainly responsible. The chief factors are considered briefly below; where any two factors seem to be causally connected, they are considered together.

(i) *Light and Depth.*

Schimper[1] states that the decisive factor in *water is light, while to heat little or no importance attaches*; Schiller[2] holds that light and probably also the salt-content are the determining factors. At all events, since the "producers" of the sea utilise solar energy as a source of anabolic power, such organisms will tend to dispose themselves both in time and place with regard to the same, such reaction not of necessity being a positive one. "Probably the vernal increase in phytoplankton depends on the rapid increase of the amount of solar energy which accompanies the lengthening days of early spring, especially about the vernal equinox" (**5**).

If the sunshine curve for Aberystwyth waters be considered (Fig. 3), it will be seen that there is a general but by no means marked agreement with the volume of phytoplankton. Indeed, during the winter months, the volumetric variation seems to follow the temperature curve rather better. This divergence for the winter months is probably directly attributable to the fact that the more intense insolation in the summer months has a greater actinic value to the phytoplankton than the relatively impotent oblique rays towards the winter solstice. The influence of sunshine appears to be due rather to intensity of light than to duration.

Now the efficient plankton organism contrives to maintain itself floating

[1] **Schimper.** *Pflanzengeographie auf physiologischer Grundlage*, Jena, 1898.
[2] **Schiller.** "Vorläufige Ergebnisse der Phytoplankton-Untersuchungen auf den Fahrten S.M.S. *Najade* in der Adria." *Sitzungsb. Kais. Akad. Wiss. Wien*, **122**, 1913. Ref. in this JOURNAL, **2**, 1914, p. 124.

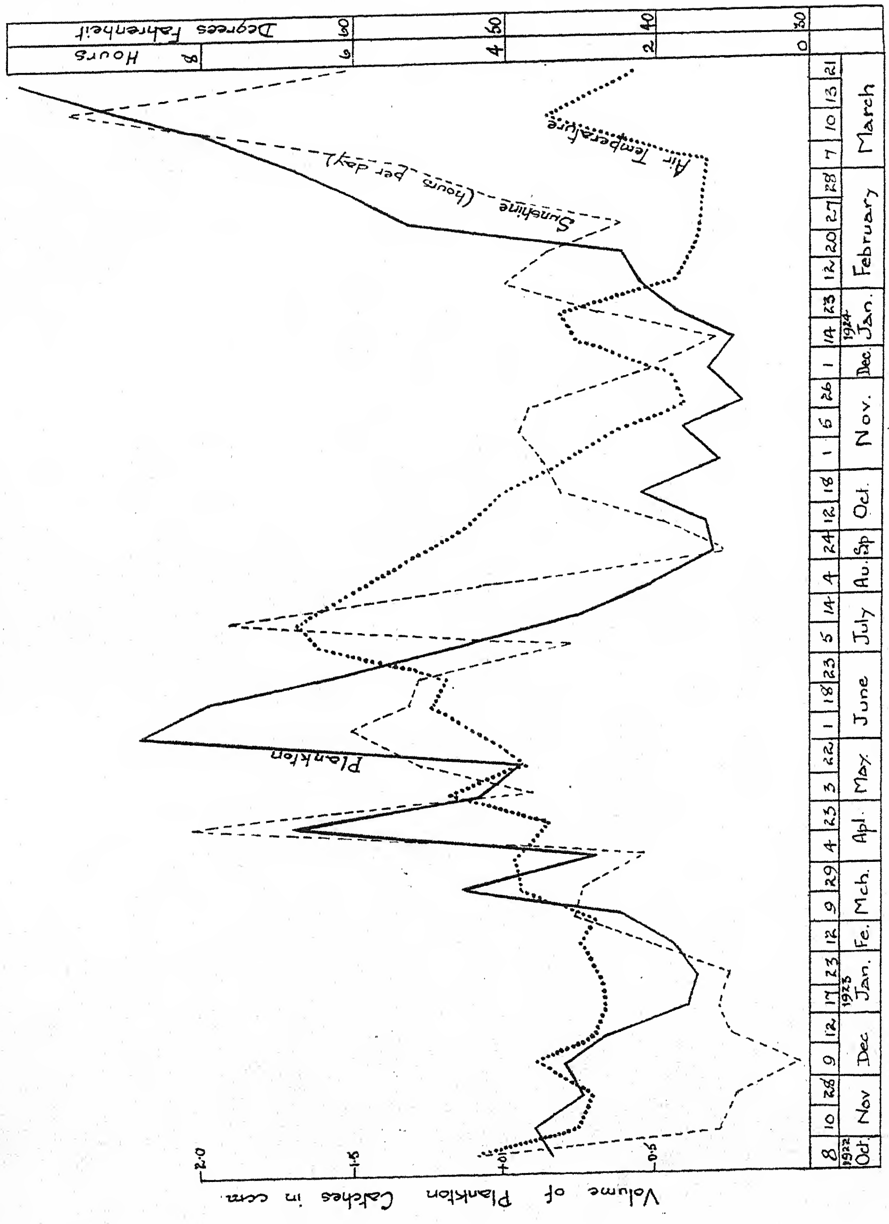

FIG. 3. Table showing relation of volume of plankton to sunshine and temperature. Catches made off Aberystwyth, Cardigan Bay; other data from Meteorological Office Reports.

at or near the surface, where the sunlight is naturally strongest. The less successful are found at lower and less bright levels, and exhibit a progressive variation in endochrome. Species common in the uppermost layers guard against excessive illumination by the movement of the chromoplasts along the plasmatic strands so as to be mutually protective. Those forms of the topmost water-layers are characterised by the possession of bright yellow-green chromoplasts, usually small and discoid, with a central pyrenoid; *Rhizosolenia* and *Chaetoceras* are the foremost examples of this group. The contrast is the more striking when the two types are compared *en masse*. Viewed in bulk, a surface catch of *Rhizosolenia* and *Chaetoceras* is several shades lighter than a sub-surface haul of *Coscinodiscus* and *Biddulphia*.

Bottom forms are for the most part pennate, and are characterised by the possession of dark yellow or brown chromatophores. These are not truly planktonic, but are often present in catches taken over shallow waters, especially in rough weather.

(ii) *Temperature.*

Temperature appears to affect the spatial distribution of the plankton, in so far as differences of temperature in the sea set up oceanic currents which are largely responsible for the geographic distribution of plankton forms. With regard to the seasonal distribution, however, we must take into account the fact that the phytoplankton rise takes place when the sea is at its coldest in March, with a second rise when at its warmest in September. Obviously then temperature is not a prime factor affecting the periodicity of the phytoplankton. "The predominant assumption in the literature dealing with algal periodicity is that these periodic changes are due chiefly to temperature variations; it makes one suspect that the real underlying causes are factors which normally operate during cold weather, but which may have no causal connection with temperature" (**9**).

(iii) *Winds, Tides and Currents.*

The indirect influence of winds on plankton distribution by setting up surface-streaming is naturally considerable; local currents and tidal-streaming are largely dependent on these. At the same time, it is debatable as to how far the distribution of plankton is limited by such streams. It has been maintained that these passively floating forms are cast up on the edges of marine currents in much the same way as a river casts up scum and floating objects on its banks; that is to say, that the plankton is disposed in "streaks" or lenticular areas with their long axes parallel to the currents in question.

A second aspect of the effect of tides and winds on the plankton is the mechanical one of increased aeration of the water. It is a well-known fact that flagellated Chlorophyceae tend to develop in enormous numbers in rain-puddles, as, in its passage through the air, the rain dissolves a high proportion of oxygen from the air. Similarly, the beating of the waters into surf-crested

waves, or even the rippling of the surface, makes for the solution of a higher proportion of dissolved oxygen and other atmospheric gases in the sea-water; this induces increased metabolic activity on the part of the contained organisms. In like manner, the waters of rapidly-moving currents tend to have a higher quantity of dissolved gases; "it is well-known that in coastal waters favourite line-fishing localities are where strong tides run through narrow channels over rocks and banks, and these are just the places where of recent years it has been found that plankton is most abundant[1]."

(iv) *Salinity and Rainfall.*

These two factors are closely connected, for, although the direct effect of rainfall in lowering the salinity of the sea is negligible for all but the topmost layers, its influence is considerable in its swelling of the volume of the rivers, and hence lowering the salinity for miles off their embouchures. Herdman states that "a heavy fall of rain, sunshine, alternation of night and day, and such phenomena probably have a considerable influence on the vertical distribution of plankton." In practice, tow-nettings made during or after a heavy rain show a drop in volume; this, however, may be due to a purely mechanical cause, namely, the difficulty of tow-netting in a rough sea, or possibly the question resolves itself into a physical one; that is, the sudden lowering of the salinity of the topmost waters would cause the passive plankton forms to sink to lower layers of greater salinity. Apart from this, variation in salinity appears to have no deleterious effect on plankton considered as living organisms; Allen (**1**) states that, provided that the conditions of light, temperature and mineral foods are favourable, salinity may be varied within very wide limits.

No single factor then appears to control the periodic disappearance of certain phytoplankton species; Johnstone, addressing the British Association in 1923, stated that "the factor influencing actual abundance appears to be a statistical one, a chance association of sub-factors, and not at all any single events, or even a few main events in the sea." Again, this periodicity has been stated to be a purely vital phenomenon entirely independent of external factors: "I therefore class this periodic growth, these....cycles which cause volumetric pulses, under the head of internal factor. The element of periodicity in itself does not seem to be consequent upon any known external factor" (Kofoid).

V. EVOLUTION OF THE PLANKTON DIATOM FORM

"The beginnings of botany," writes Church, "are in the sea." In considering the development of living matter from the non-living ionic marine phase, he has presented a scheme of progressive evolution from the specialised ionic "centres of action" in the sea, to the primitive spheroidal protoplasmic unit, and thence to what he designates the "euglenoid phase of flagellar activity."

[1] Herdman, Scott and Lewis. "Intensive Study of the Plankton round the South end of the Isle of Man, Part VI." *Reports of the Lancashire Sea Fisheries Laboratory*, **21**, 1912.

The main line of evolution progresses towards, and by way of, the benthic habit; but, in the world of free-floating forms, the euglenoid phase leads, if we except only a few isolated forms, to ultimate divergent specialisation in (*a*) the dinoflagellata, and (*b*) the now a-flagellated diatomaceae.

At the present day both these groups are racially impotent, and probably therefore represent termini of evolutionary branches. The phytoplankton organism is a highly specialised but now necessarily static form, for conditions are such that as plankton it is physically impossible for an organism to advance beyond the unicellular stage, and specialisation with the single cell as unit of somatic organisation invariably leads along an evolutionary *cul-de-sac*. In both the diatomaceae, then, and the dinoflagellata, we have groups which have succeeded in maintaining themselves as free-floating organisms since pre-benthic times. For new phyletic developments we must look to those forms which have adopted the fixed habit as opposed to the planktonic.

An attempt is here made to consider the general relationships within the most important phytoplankton phylum in North temperate seas, namely the diatomaceae.

Schütt and others state that the phytoplankton, more especially the diatoms, attains its optimal development in relatively shallow areas not far removed from land. Now the benthic is held to be a post-planktonic stage in racial evolution; in considering the development of the former from the latter, the question therefore arises of the inter-relationship of the phytoplankton with terrestrial factors. As the sea receded, and pristine land masses appeared, moribund plankton forms, it is presumed, acquired a new lease of racial life by adopting the benthic habit; they became either species fixed at the margins of the water, or motile forms creeping along the floor of the shallow coastal seas. The first assumption of the benthic habit, then, would appear to date from, or just before, the first elevation of land.

In considering the geographical distribution of the plankton diatoms, we note the fact, recorded since the days of the *Challenger* Expedition, that they are especially abundant in areas of low salinity with a high nitrate, phosphate and organic content—more especially those seas where large rivers empty themselves. From a consideration of this fact it is therefore suggested that, although these plankton diatom forms may have existed as such beforehand, yet the plankton phase *par excellence* followed *after* terrestrial elevation had taken place, and *after* water erosion had carved out the rivers. Some groups of the phytoplankton therefore may at least be coeval with, if not of later origin than, the primitive benthic protophyte. At all events, the terrestrial factor was undoubtedly a significant one.

In considering the phyletic units of the phytoplankton, it is a significant fact that those forms which compose by far the greater bulk of the tow-net catches throughout the year belong to only four genera, namely, *Rhizosolenia*,

Chaetoceras, *Biddulphia* and *Coscinodiscus*, but that these genera comprise numerous species. If numerical superiority is any measure of success, then these may be held to represent the uppermost limits of evolution among the phytoplankton. For an elucidation of the course of any such evolution one should look, not to these pre-eminent forms, but rather to those static residual genera of only one or perhaps two species, which have apparently had only a moderate success in the plankton phase. Such forms are: *Stephanopyxis turris*, *Lithodesmium undulatum*, *Streptotheca thamensis*, and *Eucampia zoodiacus*. The first-named has a valval corona of protuberances through which protoplasmic connections are stated to pass into the neighbouring frustule; in the second case, the frustules are united in long filaments bearing a superficial resemblance to a filamentous brown alga; the last two examples possess a rudimentary central nodule—all these being tentative developments towards a somatic organisation of increasing complexity. Whether these are instances of parallel development, or whether they indicate the protodiatom forms from which the plankton diatom proper, the phytobenthon and epiphytic diatoms respectively have diverged, is naturally not determinable from morphological evidence alone. At all events, there are two distinct phyletic tracks, with also a third less marked, for the phytoplankton form as seen in the sea to-day.

(i) *Typical Diatom Forms—widely distributed abundant species.*

The typical plankton forms comprise those highly successful widely distributed genera of many species which are very variable in form and which correspond to such "critical" genera among land plants as *Rubus* or *Hieracium*. To this class belong the four genera enumerated previously, namely, *Rhizosolenia*, *Chaetoceras*, *Biddulphia* and *Coscinodiscus*.

Among aquatic phanerogams, the ease with which the necessary foods are obtainable results in morphological degeneracy; in the phytoplankton, however, this relative abundance of water and nutrient salts is more than counterbalanced by the physical necessity for adequate flotation-equipment. Those forms then found free-floating in large numbers are those which have succeeded in maintaining a suitable plankton-soma—usually as the unicellular individual.

Both *Rhizosolenia* and *Chaetoceras* are genera with wide specific variation, the former consisting of about 60 species and the latter of well over a hundred. In each the elongated form is assumed; in *Rhizosolenia* this is accomplished by the intercalation of numerous plates between the valves, resulting in an enormously lengthened girdle view. In *Chaetoceras*, although each frustule is as broad as long, the individuals hang together by spinous outgrowths, giving here again the slender and long floating form. The social habit is then the rule in the latter case, whereas it is the exception in the former. Each genus has one species which has gone along a specialised line in the evolution of the

plankton-soma, and has adopted the "coiled" habit. In *Chaetoceras sociale* the frustules are grouped in an open circle, the incurved setae giving to the colony a disc-form strengthened by the ribs directed radially towards the centre, and also by the production of mucilage. In *Rh. stolterfothi* the frustules are curved, and the chains of cells thus overlie one another in a loose spiral (Fig. 2 a). These two species show development parallel with the coiled limnetic habit adopted by *Mougeotia* and other Conjugatae, when found free-floating in freshwater lakes.

Both *Rhizosolenia* and *Chaetoceras* are pre-eminent in numbers of species and individuals; at the same time, they are found in greatest numbers at the surface. These two genera then appear to be the optimum expression of the plankton habit among the diatoms of the sea.

At a somewhat lower water-level are *Biddulphia* and *Coscinodiscus*, forms moderately bulky in proportion to the surface area, and hence less mobile. They are less mobile in the evolutionary sense also, for their component species are much more static and more exactly delimited than the above-named. It follows therefore that they are of a lower grade in order of plankton efficiency; moribund species then, to ensure the continuity of their racial life, must perforce adopt a non-planktonic mode of life—and this is what appears to have happened. No species of *Rhizosolenia* or *Chaetoceras* occur among the epiphytic littoral forms, but several species of *Biddulphia* and many of the *Coscinodiscus*-type are known.

Dealing first with *Biddulphia*, we find here a genus whose component species range in habit from the euplanktonic through varying degrees to the truly epiphytic. *B. mobiliensis* and *B. granulata* are true plankton species (Fig. 4 a, b, f), as witnessed by their dorsiventral compression and valval spines and protuberances. All three species are found in the open sea. A morphologically intermediate planktonic species with absent or inconspicuous spines, abortive protuberances and ventricose valve view is *B. rhombus* (Fig. 4 c), which is especially common during the early months of the year within half-a-mile of the sea-shore. It is rarely found at any considerable distance from land, and presents a form midway between such as the three first-named species, and the characteristic coast-line species of planktonic Biddulphias, which are angular in valve view, as, for example, *B. favus* (Fig. 4 d). A closely related free-floating littoral form is the rather rarer *B. alternans* (Fig. 4 e). The resulting difference in habit is well shown by the greater silicification and more robust areolation of the former, though both species have apparently sprung from a common stock. The ultimate stage in this series is represented by the shore-type *B. vesiculosa*, which, although an occasional constituent of the littoral hemiplankton, occurs normally as zig-zag epiphytic filaments (Fig. 4 g).

The genus *Coscinodiscus* does not show so complete a series of intergrades as *Biddulphia*. They are all of the drum-like form, one of the most conspicuous

being the large species, *C. concinnus* (Fig. 1 i). Although there is little variation within this genus, a large proportion of the diatoms of the various fossil deposits are developmental forms from the *Coscinodiscus*-type, so that we have here survivors of a group that has attained considerable numbers in the past. Many of these are now extinct; this race is now represented in the plankton by certain well-defined species which have succeeded in maintaining the balance of racial efficiency in their favour.

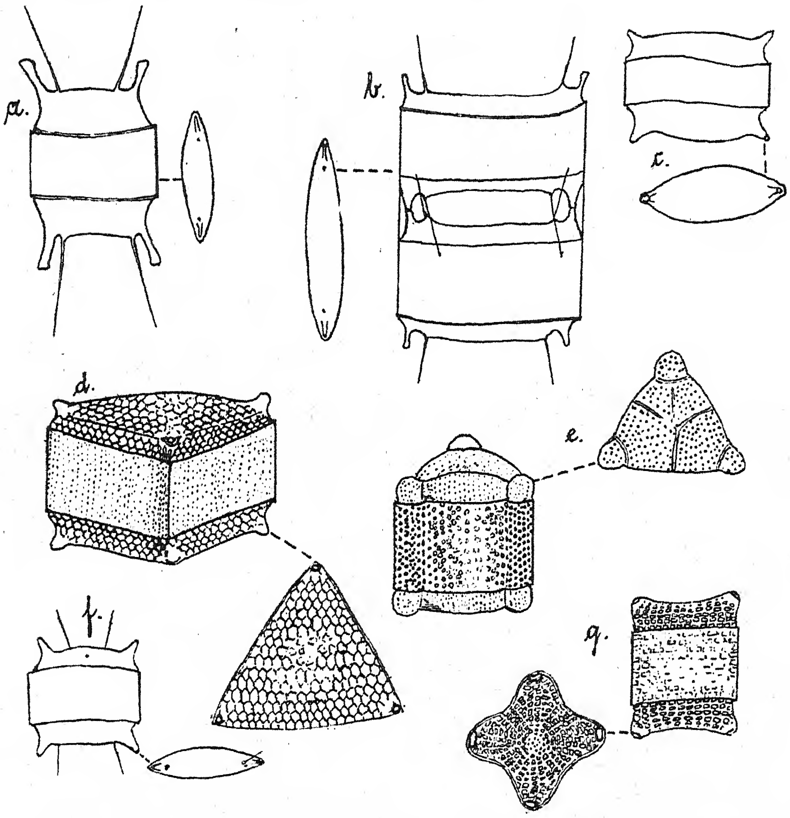

FIG. 4. Progressive variation in *Biddulphia* according to habitat. All except (*b*) × 200. N. European species. *a. B. mobiliensis* (Bailey) Grün. *b. B. mobiliensis* (Bailey) Grün. forma *regia* Schutze × 100. *c. B. rhombus* (Ehr.) Wm. Smith. *d. B. favus* (van Heurck). *e. B. alternans* (Bailey) van Heurck. *f. B. granulata* Roper. *g. B. vesiculosa* Boyer.

(ii) *Residual Plankton Forms—of less abundance.*

Turning to those isolated genera I have termed residual plankton forms, it will be noticed that the distinction from the former group is mainly one of numerical inferiority. It is from these failed and failing groups that, given sufficient impetus, new modes of life might be tentatively adopted. It has already been noted that most of the marine plankton forms are centric. Two species, *Streptotheca* and *Eucampia*, have a rudimentary central nodule. The

central nodule, important in the structure of the motile diatoms, is here apparently functionless, since they do not appear to move. Both these forms are distinct genera of limited distribution in time and place.

Two other genera, each of one species and with uncertain affinities, are *Bellerochea* and *Climacodium*. Possibly then this isolated and biologically insignificant group may be a surviving stage of the experimental forms of the early plankton phases.

(iii) *Reversionary Plankton Forms.*

The third group comprises all those forms which exhibit evidences of reversion to a planktonic from a previous benthic habit. I exclude of course such fortuitously free-floating forms as *Navicula* spp. or *Pleurosigma* spp., swirled from the bottom into the upper waters by external factors, and propose to consider only those forms which are purposively planktonic. These are all of the pennate type, and, having lost whatever planktonic adaptations they possessed in the pre-benthic state, must needs acquire a new flotation mechanism—since they cannot regain lost adaptations by retracing their evolutionary path.

This class is a well-defined group in the sea. They differ from the euplankton by the fact that they only rarely attain any great numbers—*Asterionella*, *Nitzschia seriata* and *N. closterium* are the principal ones—and that they do not show to any marked degree the bi-modal periodic curve characteristic of the phytoplankton proper. They are, in fact, comparable in many ways to the diatoms of the freshwater plankton. In both cases the greater number are pennate; in fact, the following representative list (**10**) shows both groups to comprise identical genera:

MARINE.	FRESHWATER.
Thalassiothrix (*Synedra*)	*Synedra*
Asterionella	*Asterionella*
Bacillaria	——
Fragillaria	*Fragillaria*
Nitzschia	*Nitzschia*
——	*Tabellaria*

The two first-named genera, *Thalassiothrix* and *Asterionella*, are both characterised by the union of their rod-shaped frustules into a star-shaped or occasionally zig-zag colony. By far the greater number of species of *Synedra* are epiphytic, but a few species have returned to a free-floating habit, firstly as a free-floating littoral zig-zag form, and later as a pelagic star form, which Wesenberg-Lund considers an adaptation of the former.

In contrast to these reversions from the sessile benthic to the planktonic, we have in *Bacillaria paradoxa* a retrogression from the motile benthic habit. Instead of the development of a special flotation form as in the case of

Thalassiothrix, this species has retained its power of motion to ensure a differential rate of movement in the surface-waters. As the frustules glide backwards and forwards past one another, they come into contact with different parts of the surrounding medium for nutrition, while at the same time the narrow bacillar frustules, disposed horizontally when extended, offer as much resistance as, for example, a *Rhizosolenia*, against over-rapid sinking. A similar flotation mechanism is observed in *Nitzschia seriata*, where the frustules can by gliding in the same way arrange themselves end to end in elongated series.

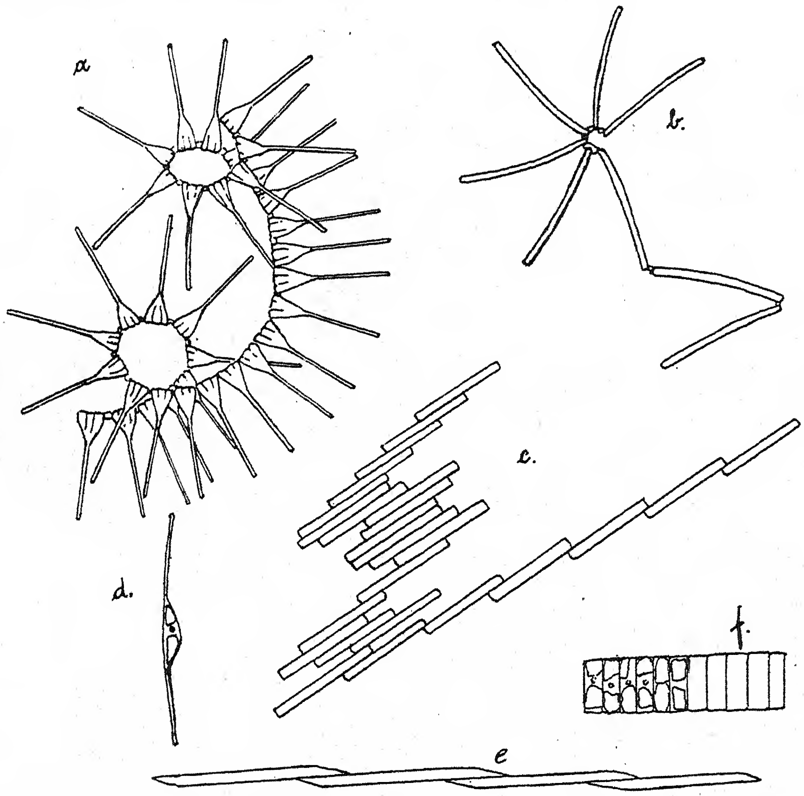

FIG. 5. Retrograde plankton diatoms. All × 200. *a. Asterionella japonica* Cleve. *b. Thalassiothrix nitzschioides* Grun. *c. Bacillaria paradoxa* Gmel. *d. Nitzschia closterium* Wm. Smith. *e. Nitzschia seriata* Cleve. *f. Fragillaria oceanica* Cleve.

The case of *Nitzschia closterium* is even more interesting. Two distinct forms are recorded. Both types are abundant in cultures; the larger is motile, but the smaller non-motile. Furthermore, in vertical plankton hauls containing a bigger proportion of bottom forms than horizontal hauls, the latter variation of *N. closterium* is more frequent. Lebour[1] states that this is an adult form

[1] **Lebour, M. V.** "The Microplankton of Plymouth Sound." *Journ. Marine Biological Association*, 1917.

of the smaller one. Here then we appear to have in the plant world an organism with two stages in its life-history, a planktonic followed by a benthic stage, this being analogous with those marine animals such as *Balanus*, whose larval stages are free-floating, but whose adult forms are benthic.

The above is an attempt to indicate that the term plankton, as far as the diatoms at least are concerned, comprises a polyphyletic assembly of species with different racial history but similar habit; or, as Church has said, "Plankton is more physiological than morphological."

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THE WATER-RETAINING POWER OF THE SOIL

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(With three Figures in the Text.)

By the water capacity of a soil is understood the quantity of water which a given soil is capable of retaining. It is expressed as a percentage of the volume of that soil.

There is considerable variation in the water capacity, according to the size of the soil particles. The more finely divided the soil, the higher its water capacity, as will be seen from the following table (from *Boden und Klima auf kleinstem Raum*, by G. Kraus):

Table I.

Percentage of soil particles larger than 0·5 mm.	Water capacity
89·7	9·19
89·5	10·5
82·72	14·51
58·19	18·6
56·6	19·34
31·0	29·4
17·02	30·26
0 (washed soil)	28·0–52·0

Of the water thus retained by the soil, a portion remains adhering to the soil particles as a thin layer held by adsorption, while the rest collects in small hollows and crevices, where it is retained by capillarity. Gradually, as the amount of water in the soil becomes less—as a result of evaporation, for instance—the water held by capillarity will be the first to disappear, then the water retained by adsorption. While the retaining power of the capillarity is only slight the adsorbed water is held back with rather considerable force.

For a plant to be capable of drawing water from the soil, the force with which it sucks up the water must be stronger than that with which the soil holds the water back; and the results of numerous experiments go to show that plants are generally capable of absorbing the water that is held by capillarity, but not—or, at most, only partly—the water held by adsorption. If, now, a plant of some kind is grown in the soil, without any more water being supplied to the latter, the quantity of water which the soil contained at the beginning of the experiment will gradually be reduced, until the plant finally wilts, because the absorptive force of the roots can no longer overcome

the water-holding power of the soil, though there will still, at that moment, be a certain amount of water left in the soil.

If specimens of the same kind of plant are grown in different soils, it is safe to suppose that the water-retaining power of these soils will be the same at the moment when the plants wilt. The water content, on the other hand, at the moment of wilting, will be different in the different soils. This is made evident by the results of an experiment, made by Sachs, in 1859, with tobacco plants:

Table II.

Soil	Original water content in 100 grams dry weight	Water content at the moment of plant wilting	
Sand and humus	46·0 grams	12·3 grams	27 % max. content
Clay	52·1	8·0	15
Coarse quartz sand	20·8	1·5	7

The result of this experiment shows the water-retaining power of the quartz sand to be rather feeble as compared with that of the clay soil or of sand mixed with humus.

For these reasons, a simple determination of the water content of the soil does not furnish any basis for a true estimation of the amount of water actually at the disposal of the plants. To determine this, it will be necessary to proceed differently; namely, by trying to determine the water-retaining power of the different soils with various contained water percentages. The present paper is an attempt in that direction.

As an introduction, let us review, very briefly, some of the earlier investigations made for the purpose of determining the water-retaining power of the soil. The methods employed to that end have been partly physical, partly biological.

I. *Physical methods.* **Livingston** (1906) places in the soil to be studied an artificial root hair, in the form of a semipermeable "Pfeffer's cell," filled with a 1·5 to 2 molecular solution of cane sugar, and then determines whether this osmometer absorbs the water from the soil, or whether a movement in the opposite direction takes place. As the result of a couple of experiments it was found that the absorption, by the osmometer, did not begin until the water content of the soil was brought up to 20 or 25 per cent. **König, Hasenbäumer** and **Grossmann** (1908) placed the soil to be examined in a "Pfeffer's cell," poured water over it, and measured the osmotic pressure after the cell had been sunk in water. The figure obtained thus indicates the degree of osmotic pressure exerted by the soil water (though in a diluted state). **Shull** (1916) determined the water content of *Xanthium* seeds that had lain in the soil, and from the results thus obtained he was again able to calculate the degree of the osmotic pressure by which the water was retained in the soil, by comparing them with measurements previously made of the water contents of other *Xanthium* seeds that had been lying in solutions of various concen-

tration and of known osmotic strength. As a means of determining the water-retaining power of the soil, **Livingston** and **Koketsu** (1920) measured the amount of water absorbed within a given time by a hollow, cone-shaped cylinder of porous porcelain. Other investigators, like **Van Bemmelen** (1910) and **Odén** (1919), determined the vapour pressure in humus by placing the dried sample of soil in a desiccator over a sulphuric acid solution of known concentration and vapour pressure. When equilibrium has been attained, the water content of the sample is determined, and it is then placed in another desiccator over a slightly more concentrated solution of sulphuric acid. When the equilibrium is once more established, the water content of the sample is determined a second time; and by continuing in this manner and noting, one after another, the values thus obtained, a curve will result, showing the dependence of the vapour pressure on the water content of the humus. **Thomas** (1921) estimates the water pressure in three different soils. His method consists in passing a known volume of air through the soil, collecting and weighing the vapour. He finds that the vapour pressure is a linear function of the reciprocal of the moisture content over a wide range.

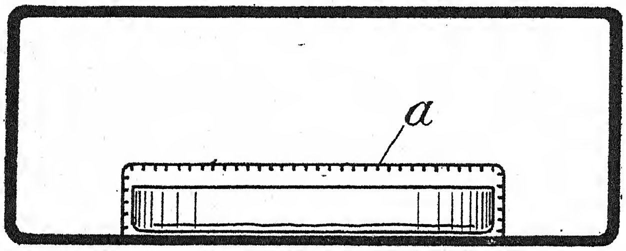

FIG. 1.

II. *Biological methods.* **Briggs** and **Shantz** (1912) determined the wilting coefficient for various soils by the "wax-seal method," which is a modification of the method formerly employed by **Sachs**. They find this coefficient to be about the same for a number of different plants, and note that it varies considerably with the character of the soil. **Ursprung** and **Blum** (1921) find the water-holding power of a soil by determining the absorptive power of a root that has grown in it, because these two quantities must be supposed to be equal. The absorptive power of the root is measured by determining the volume of an epidermis cell in its natural state and then measuring the concentration of the cane sugar solution which does not alter the volume of that cell. The water-retaining power of the soil will then be equal to the osmotic pressure of the cane sugar solution.

The method which I have used for measuring the water-retaining power of the soil consists in determining the strength of the sugar solution which has the same vapour pressure as the soil sample under investigation.

The procedure is as follows: in a glass box, 16 × 6 × 11 cm., with a loose glass lid, a piece of nickel-wire netting (a in Fig. 1) 9·5 cm. high by 15·5 cm.

long, and having 2·5 cm. of this length, at each end, bent over at right angles, is placed in such a manner that the bent-over edges rest against the side of the box, forming a small cage, as shown in Fig. 1. The glass box is thus divided into two compartments of unequal size. The soil to be investigated is placed in the larger of these, whereupon the lid is sealed on air-tight by means of vaseline, and the closed box placed in another, larger box lined with cotton

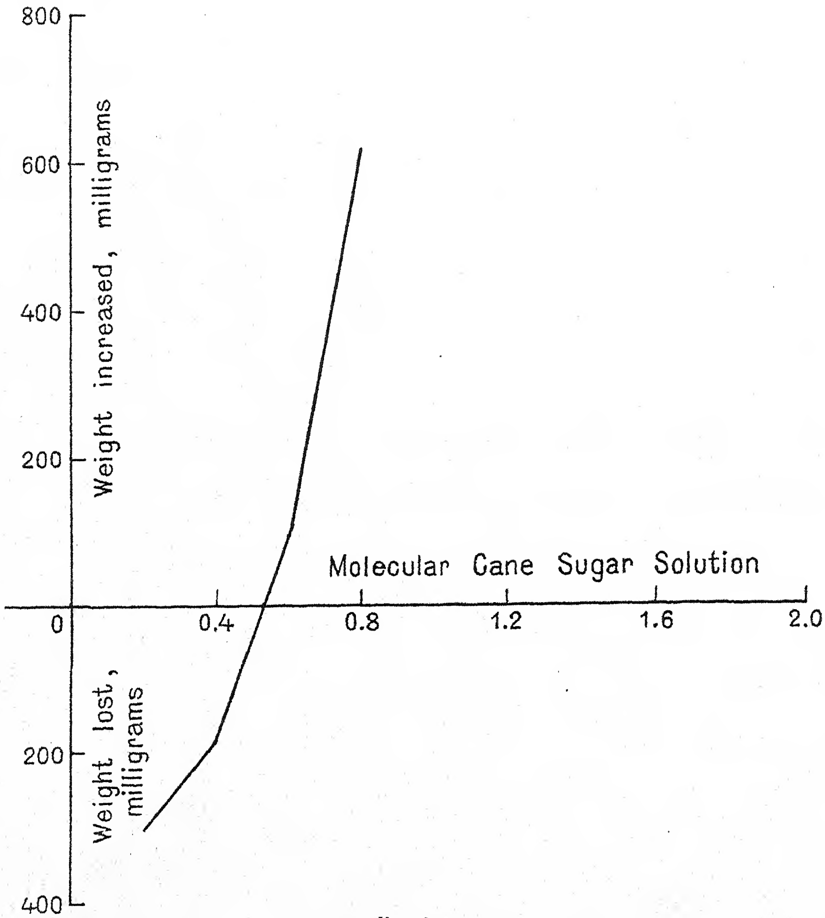

FIG. 2.

wadding, for 24 hours. After that time the glass box is taken out and opened, and in the smaller compartment is placed the bottom part of a Petri dish, 10 × 1 cm., on the inside of which has been laid a paper filter saturated with a cane sugar solution of a previously determined strength. The lid is then sealed on again with vaseline, and the glass box put back in the wadding-lined receptacle for another 24 hours. After that time the box is opened once more, the Petri dish is taken out, and the lid is put on again. The Petri dish with

the filter is now weighed, and if a similar weighing has been made before the test was begun, it can be ascertained whether the sugar solution has absorbed or given off water; or, in other words, whether the vapour pressure of the sugar solution has been greater or less than the vapour pressure in the soil investigated. If, now, we extend the experiment to comprise—instead of only one glass box, as here described—four or five boxes, all containing the same kind of soil, but with the sugar solution in a different degree of concentration for each of the filters, we shall find, provided these concentrations have been suitably chosen, that the Petri dishes containing the weaker solutions have lost in weight, while those containing the stronger concentrations have become heavier; and by these means it will thus become possible to determine exactly what sugar concentration has the same vapour pressure as the soil under investigation. The easiest way of arriving at this determination is to make it graphically, by plotting the rate of change—that is, the loss, or the increase, in weight—corresponding with the different concentrations, on squared paper, and constructing a curve connecting these various points. The point at which this curve intersects the axis of the abscissae will then mark the degree of concentration of the sugar solution with which the soil sample is in equilibrium.

By thus examining a number of samples, all from the same soil but of different water content, we get, in this manner, an expression for the relation of water-retaining power to water content, in the soil type examined.

Variations in temperature are the chief sources of error in connection with these investigations. If, namely, the soil sample and the sugar solution in the Petri dish are of different temperatures, an over-distillation of water may take place, even if the vapour pressure should be the same in both. Every precaution must therefore be taken to avoid the occurrence of any such variations, and this is done by isolating the glass box as carefully as possible in the cotton-lined outer box, as described.

In order to test the correctness of the method, there were placed in the arger compartment of the glass box strips of paper saturated with an equimolecular potassium nitrate solution, and in the Petri dishes potassium nitrate solutions having a concentration of, respectively, 0·5, 1·0 and 1·5 gm. molecules. The result is shown in Table III.

Table III.

	0·5 mol.	1·0 mol.	1·5 mol.
Experiment I	−0·08	—	+0·065
Experiment II	−0·07	0·0	+0·06

The experiment shows that it is possible to measure more or less approximately the osmotic pressure of a given solution.

By this method I have investigated the reciprocal relation between the water-retaining forces, together with the water content of five different types of soil.

Experiment I. In this series of tests a *pure quartz sand* with a water capacity of 14 per cent. was used. The result of the experiment is given in Table IV:

Table IV.

Water content (%)	4·4	1·84	1·09	0·56	0·21
Mol. cane sugar solution	0	0·42	0·51	0·91	1·82
Osmotic pressure in atmospheres	0	11	14	28	90

Experiment II. The soil used in these tests was *sand mixed with clay.* The sample was entirely free from humus, and on being washed was found to contain 62 per cent. of sand, with a water capacity of 27 per cent.

Table V.

Water content (%)	10·74	7·18	4·81	4·28	3·25	3·15	2·17
Mol. cane sugar solution	0·06	0·18	0·67	0·86	1·35	1·53	1·84
Osmotic pressure in atmospheres	1·5	4	19	26	51	63	92

Experiment III. These tests were made with *garden soil* containing 62 per cent. of sand and 5·25 per cent. of humus. The water capacity was 24 per cent.

Table VI.

Water content (%)	19·35	12·39	9·49	8·66	7·04	6·18	5·67	5·06	4·54
Mol. cane sugar solution	0·1	0·2	0·25	0·3	0·74	0·96	1·24	1·58	1·93
Osmotic pressure in atmospheres	2	5	6	7·5	21	30	45	67·5	100

Experiment IV was made with *pure clay* (modelling clay).

Table VII.

Water content (%)	29·68	23·84	20·47	17·32	13·83	12·1	9·92
Mol. cane sugar solution	0·02	0·06	0·24	0·34	0·51	1·21	1·91
Osmotic pressure in atmospheres	0·5	1·5	6	8·5	14	43	98

Experiment V. In this experiment the soil was *beech mould.* The water capacity was 61 per cent.

Table VIII.

Water content (%)	36·45	29·32	24·0	23·47	19·0	15·83
Mol. cane sugar solution	0·24	0·38	0·44	0·5	0·74	1·7
Osmotic pressure in atmospheres	6	10	12	13·5	21	83

The results of these experiments are represented graphically in the following curves, in which the abscissae denote the water content of the soil type in question, while the ordinates denote the cane sugar solution, or the osmotic pressure corresponding to the various concentrations.

As we might expect from the results of **Sachs'** experiments, the water-retaining power of the sand is extremely slight; only with a water content of 1 per cent. does it reach a strength equal to the osmotic force in a 0·5 molecular cane sugar solution, which corresponds to a pressure of 13 or 14 atmospheres. If we suppose the osmotic pressure at the beginning of plasmo-

lysis in the roots to be about 10 atmospheres, then the intake power also should consequently run no higher than to this value as a maximum; which is equivalent to saying that the absorption of water by the roots ceases when the water content of the soil has sunk to 2 per cent.—a proposition which agrees fairly well with the findings of **Sachs**, that tobacco plants wilted when the water content was 1·5 per cent.

A comparison of the curve for the pure quartz sand with the one for the sand mixed with clay shows that the clay content plays a great rôle as regards the water-retaining power, the latter rising, owing to the presence of the clay, to as much as 13 or 14 atmospheres when the soil contains 5·5 per cent. of water. With a lesser content of water the retaining power of the sand and clay mixture rises somewhat less rapidly than in the pure sand.

The soil which forms the subject of experiment III differs from the one used in experiment II chiefly by its content of humus, and it is noticed that this admixture tends to increase the water-retaining power, which here, for a water content of 8 per cent., reaches between 13 and 14 atmospheres.

It is in pure clay and pure humus that the water- holding power is greatest. In beech mould, as shown by experiment V, it is as high as 13 or 14 atmospheres with a water content of 23 or 24 per cent. As a curious feature it should be noted that with decreasing water content the increase in water-retaining power is much slower here than in the first three experiments.

By this method it is possible, then, to determine more or less approximately

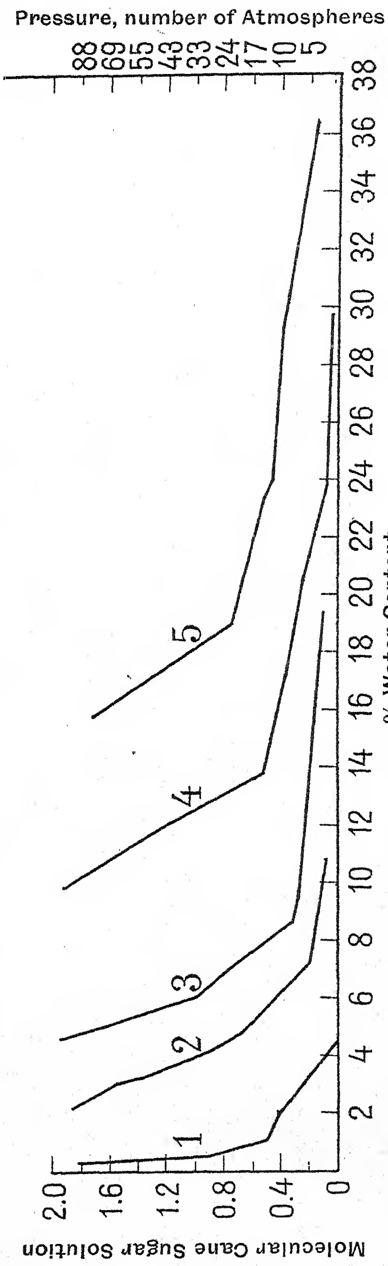

FIG. 3. Curves showing the water-retaining power in different soils; (1) pure quartz sand; (2) sand mixed with clay; (3) garden soil; (4) modelling clay; (5) beech mould.

the vapour pressure in any given soil, and thus the water-retaining power of that soil. It next becomes a question of examining what importance the degree of that power has for the absorption of water through the root system.

For a root to be able to absorb water from a given soil it is necessary that the force with which the absorbing cells of that root suck up the water should be greater than the force by which the water is held back in the soil. The absorptive power of the cell is, in its turn, determined by the strength of the osmotic pressure, less the strength of the sap tension, by which is understood that portion of the osmotic pressure which is exerted on the wall of the cell. The absorptive power can thus vary from zero up to the value of the osmotic pressure exerted under conditions of commencing plasmolysis. As a result of this absorption by the cells the water content in that part of the soil which is in immediate contact with the surface of the root is reduced to a quantity so small that the force by which the water is retained in the soil is equal, or only slightly inferior, to the force with which it is absorbed by the plant. In those parts of the soil which are farther away from the surface of the root, the quantity of water will be greater, and this difference in water content between the different regions of the soil, due to the absorption from the root, will therefore result in a movement of water from the more distant, moister regions toward the surface of the root. It is this movement of the water in the soil which enables the plant to continue its absorption of water. Any increase in the absorptive power of the cell will cause the amount of water in the part of the soil in immediate contact with the root surface to become still further reduced, and the difference in water content between the different parts, which causes the water movement, will thus be all the greater.

The fact that **Fitting** has ascertained the osmotic pressure in a number of desert plants to be relatively high, makes it of interest to examine in what types of soil an increase of the osmotic pressure may possibly have a bearing on the degree of absorption. A look at the curves will show that an increase of the osmotic pressure will not be of any material significance in the case of plants growing in sandy soils, because even with a low osmotic pressure these plants will be able to absorb practically all the water in the soil. In soils containing a great deal of humus or clay, or of both these substances together, and in which the water is, consequently, retained with rather considerable force, an increase in the osmotic pressure may, on the other hand, help to increase the amount of water on which the plants can draw. It is therefore of interest to see that the abnormally high osmotic pressures recorded by **Fitting** were found by him in plants that grew in rock- or desert-crevices filled with clay, while the osmotic pressure of the same plants, when they are grown in sand, is considerably less.

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OBSERVATIONS ON A LUMBERED AREA IN SURREY FROM 1917 TO 1925

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(With eight Figures in the Text.)

CONTENTS.

INTRODUCTION

During the war a considerable area of forest on the Bagshot Sands in the neighbourhood of Virginia Water was felled by Canadian lumbermen. The land was not immediately replanted and as it lay conveniently near the Royal Holloway College Botanical Laboratory, continuous observations were made to record the natural changes of vegetation over the exposed area (Fig. 1).

A plot of land was chosen for detailed study, about an acre and a half in area, sloping slightly to the south-west. It had been pure pine forest, but outside it, in its near neighbourhood, there stood a few birches among other trees, and this fact explains in part the plant succession that followed.

Observations were continued until January 1925, when the forest authorities of Windsor Great Park cleared the area and replanted it with *Pinus sylvestris*.

HISTORICAL ACCOUNT

The Area at the Outset of the Investigation in 1917.

The Canadian lumbermen had been at work from June to October 1916 and in November of the next year observations began. At this time there was very little vegetation, the uneven surface of the soil being broken only by numerous tree stumps and certain charred patches, nineteen in number, where the lumbermen had made their large bonfires. The surface of the soil was covered with loose pine needles, below which, to a depth of from 1 to 5 inches,

[1] The work described in this paper was organised and written up by M. Benson (1917–22) and E. M. Blackwell (1922–25) with the help of notes and maps made by D. M. Adkins (Mrs Burrows), 1915–20 and M. I. Thomas, 1921–25, Royal Holloway College, University of London.

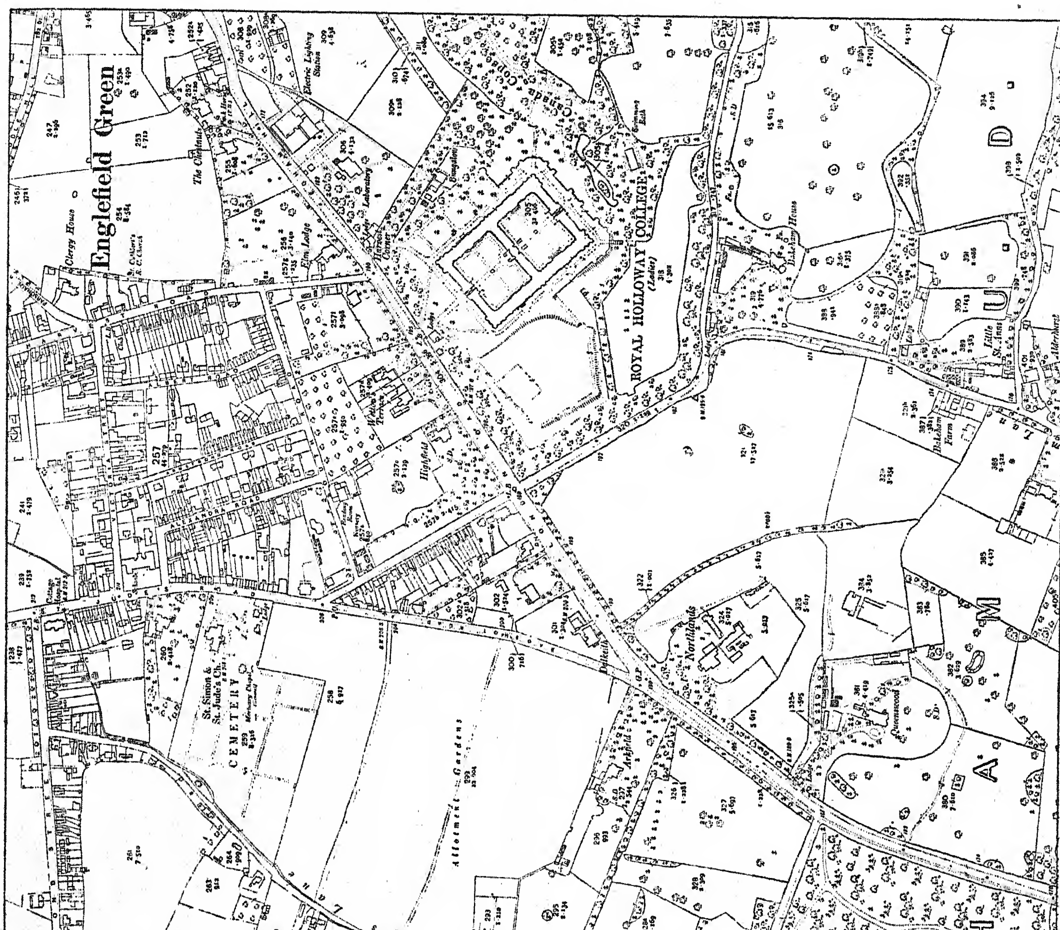

FIG. 1. Map showing the high road from Staines to Virginia Water with the Royal Holloway College on the right and the observational area outlined in the bottom corner on the left.

lay humus composed of dead pine needles, twigs and cones, and then sand varying in depth from a few inches to 4 feet. In some parts, the water level was at the junction of the sand and the subjacent clay; in other parts it was in the sand. During the course of investigation, the level of the water table was found to vary with the seasons to a very marked degree.

At the south-east corner of the plot, there was a small bog, where the water, like that in the soil in other parts of the area, was acid to litmus. Species of *Sphagnum* and *Polytrichum* grew in the bog and at the edge were three species of *Juncus*. On the banks of the bog were numerous seedlings of *Betula alba* (*verrucosa*), and *B. pubescens*, *Pinus sylvestris*, *Castanea sativa* and *Rhododendron ponticum*.

Along the north-west of the area there was a fringe of vegetation. This consisted of pine and birch seedlings of the current season, *Molinia caerulea*, *Deschampsia flexuosa*, *Erica cinerea*, *E. tetralix*, and *Calluna vulgaris*, which had secured a hold owing to a slight opening in the forest in that region. Occasional seedlings of *Larix europaea*, *Ulex europaeus*, *Castanea sativa* and *Quercus robur* (*pedunculata*), also of the current year, were noted.

The charred patches, where fires had been made, were for the most part bare, but towards the centre of each patch *Funaria hygrometrica* was beginning to establish itself.

During the autumn of this year, a remarkable feature of the plot was the luxuriant growth of *Bulgaria polymorpha*, the sporophores of which reached a diameter of 5 or 6 inches in their spread over the soil. A very few individuals of wind-dispersed immigrants, such as willow herb, and even dandelion and thistle, had arrived. With these exceptions, the land was clear of vegetation, and thus might be said to offer a new habitat for colonisation.

METHOD

The area, comprising altogether some 4980 sq. ft., was divided into 46 smaller areas; peripheral areas 20 ft., 45 ft. and 60 ft. square, and central areas of greater size (Fig. 2). Quadrat charts were made of each in 1917, 1919 and 1924. Figs. 5–8 illustrate four out of the forty-six such series made. Each year general observations were recorded in note form, and plants observed were listed.

In addition to the mapping of the whole area intensive studies were made of features of special interest, e.g.:

(*a*) The extension of each patch of bracken was measured separately.

(*b*) An intensive study was made of certain subdivisions of the above areas, e.g. of the "oases."

(*c*) An intensive study of individual species was made with reference to depth of root in the soil.

The water table was observed at intervals by noting the height of water in the bog, which frequently became a pond, and by digging in other parts.

OBSERVATIONS MADE DURING 1918

Until the late autumn of 1918, the appearance of the ground remained almost unchanged, except that the burnt patches were covered with bright green vegetation, and stood out vividly from the surrounding stretch of bare ground. The striking contrast between these patches and the barren "desert" surrounding them, suggested "oases." It is on this account that we shall use this term in our reference to them. The vegetation of the oases consisted of *Marchantia polymorpha* and *Funaria hygrometrica,* which now covered the whole of their surface.

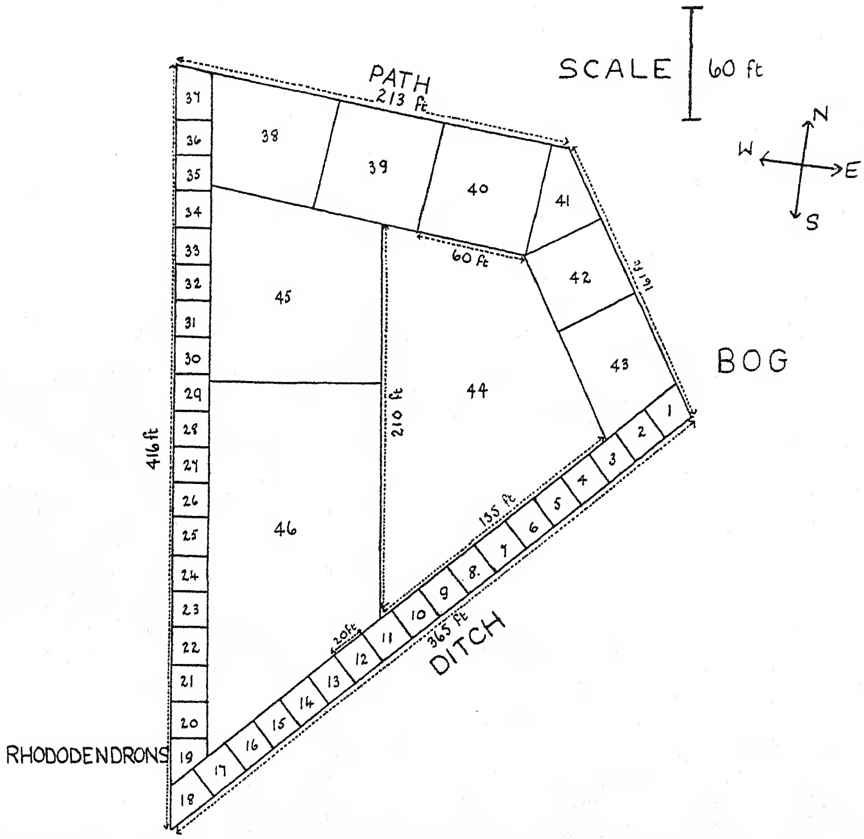

FIG. 2. Plan of the observational area divided into quadrats, etc. for map making.

Some evidence of a slight advance on the part of the peripheral vegetation was observed, and enumeration of seedlings gave a considerable increase of pines (*Pinus sylvestris*) and especially of birches (*Betula alba*).

The giant sporophores of *Bulgaria polymorpha* once again appeared, giving the area in some parts the appearance of being covered at short intervals with cow dung.

During this year rabbits were frequent visitors, as was seen by their nibbling of *Deschampsia flexuosa*, and by the gradually accumulating nitrogenous debris which they left behind them.

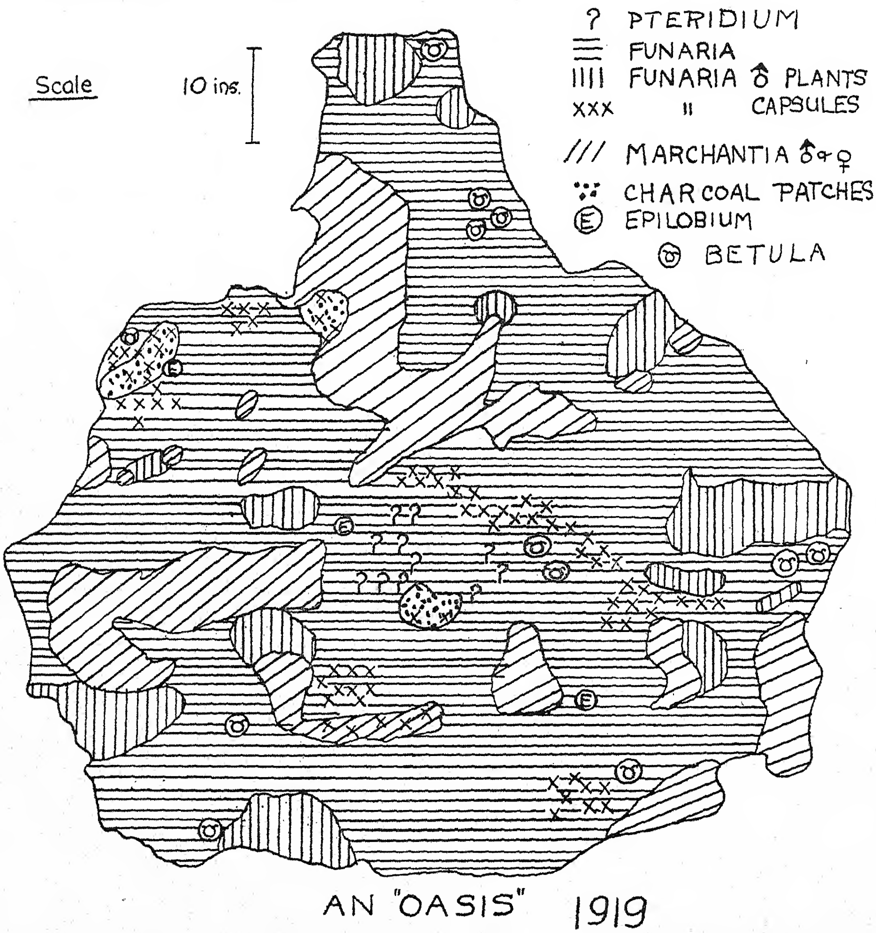

FIG. 3. Map of an oasis in 1919, illustrating the colonisation of a burnt patch.

OBSERVATIONS MADE DURING 1919

By May 1919, considerable changes had taken place, both on the open ground and on the oases (Fig. 3). The vegetation of the oases had a compact velvety appearance. Every square inch of space was occupied; indeed, in a few places the vegetation was stratified, for *Marchantia thalli* were found actually creeping over *Funaria*, and *Peltigera* was spreading horizontally over both. The *Marchantia*, which was very abundant, showed an unusually close formation of archegoniophores and antheridiophores, and was producing gemmae. *Funaria* was beginning to die down, and was covered with ripe capsules. In the centre of several of the oases, sporelings of bracken had made

considerable headway and were firmly established. Further interesting evidence of the oases being favourable seed beds was found in the variety of seedlings which had germinated upon them: for example, side by side were seedlings of a willow, a willow-herb, a holly, and a sheep's sorrel. It was most striking to find one bird-borne and three wind-borne individuals on a single oasis and only *one* example of each.

The central region of the area was almost as bare as in the previous year. As in the oases there were a few immigrants, which included two plants of clover, a few of chickweed, a few composites, and some poorly developed individuals of the rose bay willow-herb (*Epilobium angustifolium*).

In the peripheral region of the area *Molinia caerulea* was the dominant element in the vegetation, as the *Calluna* and *Erica* spp. and *Deschampsia flexuosa,* though slightly more abundant than formerly, had not increased at the same rate. Among the *Molinia* tussocks two year old birch seedlings were numerous and flourishing. The pine seedlings were fewer in number than the birches, and many of them looked unhealthy. As the result of excessive rain during the spring of this year, parts of the area were under water. The *Molinia* in these very wet parts was dead or dying.

In the bog, *Sphagnum,* although well supplied with water, was turning brown. The water in the bog was at this time neutral to litmus.

The summer of 1919 was dry, and in consequence the water table had receded, and the bog was almost dry. The increased aëration of the soil due to this change had favoured the progress of *Molinia,* which was, however, attacked by Ergot (*Claviceps purpurea*). At the outer limits of the area, with the exception of the ground immediately surrounding the tree stumps which was quite bare, *Molinia* was dominating an almost closed society.

On a few of the oases the vegetation had been uprooted and trampled down, and thus was not able to develop on natural lines. The damage was probably caused by rabbits. In the bog, *Sphagnum* had disappeared for the time being, *Polytrichum* had nearly disappeared, and a species of *Mnium* was replacing them.

No trace of *Bulgaria* was observed, although it had been so abundant the two previous autumns, nor has this fungus again appeared on the plot.

Throughout the area, various seedlings, many fungi, and a moss, *Campylopus flexuosus*, occurred occasionally, and served to break the otherwise uniform dark colouration of the bare regions.

OBSERVATIONS MADE DURING 1920

As the result of heavy rains during November and December 1919, the area was wet in the spring of 1920. In runnels washed out by the surface drainage during heavy rain, seeds of *Molinia* had germinated readily, and thus young *Molinia* plants occurred in straight lines as though produced by rhizomes. The *Molinia,* which was originally peripheral, now covered a

considerable part of the area. *Erica tetralix* and *Calluna vulgaris* were still associated with it, and were in a few localities even abundant. *Deschampsia* occurred frequently, but usually the foliage had been nibbled by rabbits. The pine seedlings were few in number, and unhealthy, except those on an elevated part of the bog margin.

Now for the first time were noted the ravages of the pine weevil in the pine stools; and it was found that some of the pine seedlings had been partly eaten. The birches on the other hand were very numerous, and some of them reached a height of five feet.

In October, *Sphagnum* appeared again in the bog. This was found to be coincident with a change in the bog water from neutral to acid reaction.

Some of the oases, though still velvety, had a different floristic content, for *Funaria* and *Marchantia* had been succeeded by *Dicranum longeanum*, a moss common on the Bagshot Sands. *Barbula fallax*, *Campylopus flexuosus*, *Hypnum purum* also occurred. The bracken on the oases was spreading rapidly, and appeared to be well established. As the *Molinia* advanced, it surrounded some of the oases, and eventually invaded them, the invasion being made easier no doubt by the previous breaking up of the surface by rabbits. The central part of the area was in parts dotted with young *Molinia* plants. A few specimens of species of *Erica*, *Calluna*, *Deschampsia*, and *Rumex* occurred, and *Campylopus flexuosus* was so prevalent, that in some places the ground was of a uniform green colour. No fruits of this moss were observed, but a method of propagation by detached branches, formerly recorded by Rabenhorst, may account for the rapidity of its distribution. If one draws a finger lightly over the surface of the moss, large numbers of short detached branches are thrust up, and lie free on the surface. This takes place so definitely, that one can mark out a design on the surface of the moss. These freely exposed branches can be blown away by the wind. If, on the other hand, the finger is drawn rapidly and with some slight pressure over the moss, the free branches spring up elastically, owing to the compressed condition of the upper stratum, as compared with that of the lower, and shoot to a considerable distance. Thus the scurrying of rabbits across a patch of *Campylopus* results in the wide distribution of leafy branches, which quickly establish themselves by rhizoids. This characteristic of *Campylopus* may account for its hold over the long exposed central region, which for some reason or other never became colonised by germinating seeds and spores.

OBSERVATIONS MADE DURING 1921

In the early part of this year, colonisation received a check as a result of fire. Many seedlings were scorched and birches injured and some of the pines completely destroyed. The injury to the *Molinia* was not fatal. Oases with their established bracken escaped, as *Campylopus* was incapable of spreading the fire. The bracken (*Pteridium aquilinum*) was growing radially out from

those centres where sporelings had previously been noted. There were only five oases on which bracken had failed to establish itself, and only five patches of bracken in places which had not formerly been burnt areas. Thus the great majority of established plants of bracken were strictly limited to the oases. On one of these *Marchantia* was growing well and bearing old archegoniophores.

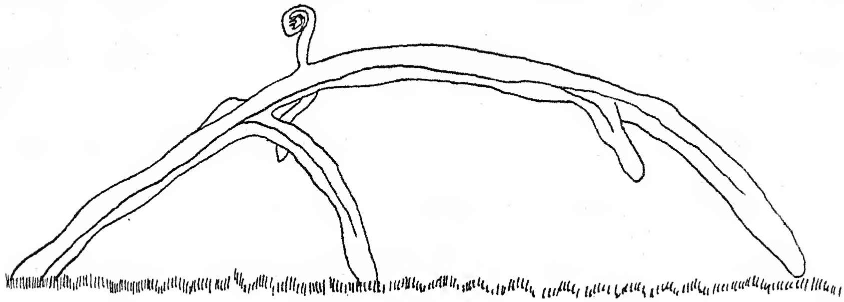

FIG. 4 (*a*). Arching of Bracken rhizome whose apex was unable to grow forward owing to the hardness of the soil. The portion of the rhizome behind the apex has elongated and curved, raising itself above the surface of the soil from which the apex has been lifted by hand.

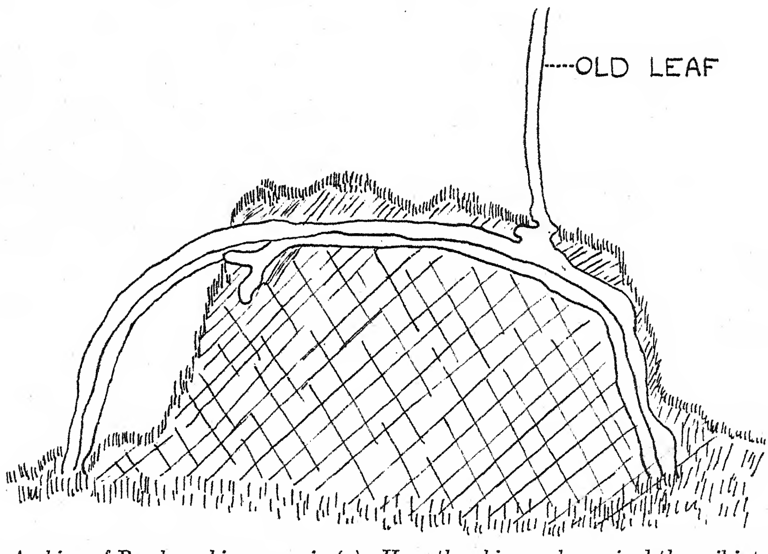

FIG. 4 (*b*). Arching of Bracken rhizome as in (*a*). Here the rhizome has raised the soil into a small hummock (indicated in section).

Another oasis was completely surrounded by *Molinia* and showed signs of yielding to its pressure, as *Polytrichum* was found brown and flattened under the tussocks.

The summer was exceptionally hot and dry and there was much evidence of the ravages of rabbits. Both *Calluna vulgaris* and *Erica cinerea* were nibbled and the covering of *Campylopus*, so vividly green and uniform in 1920, was very thoroughly broken up into fragments. As the drought continued, *Campy-*

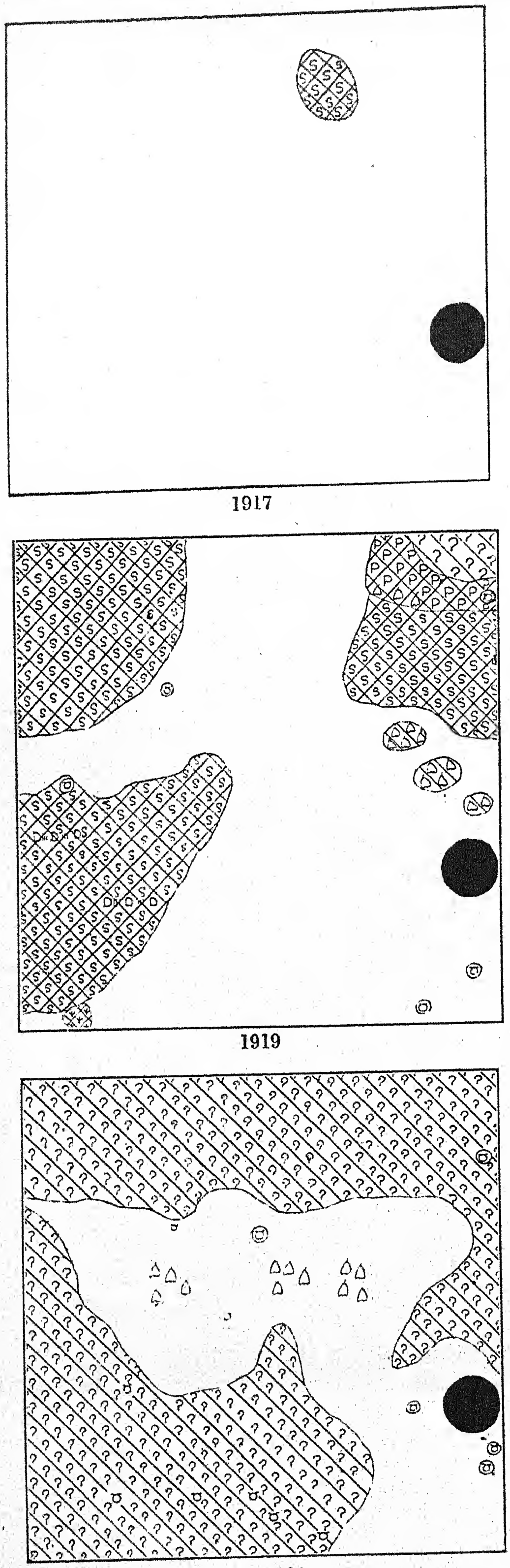

Fig. 5. Charts of quadrat 11 (20 × 20 ft.) in the years 1917, 1919 and 1924, illustrating the establishment of *Pteridium aquilinum* among Bryophyta.

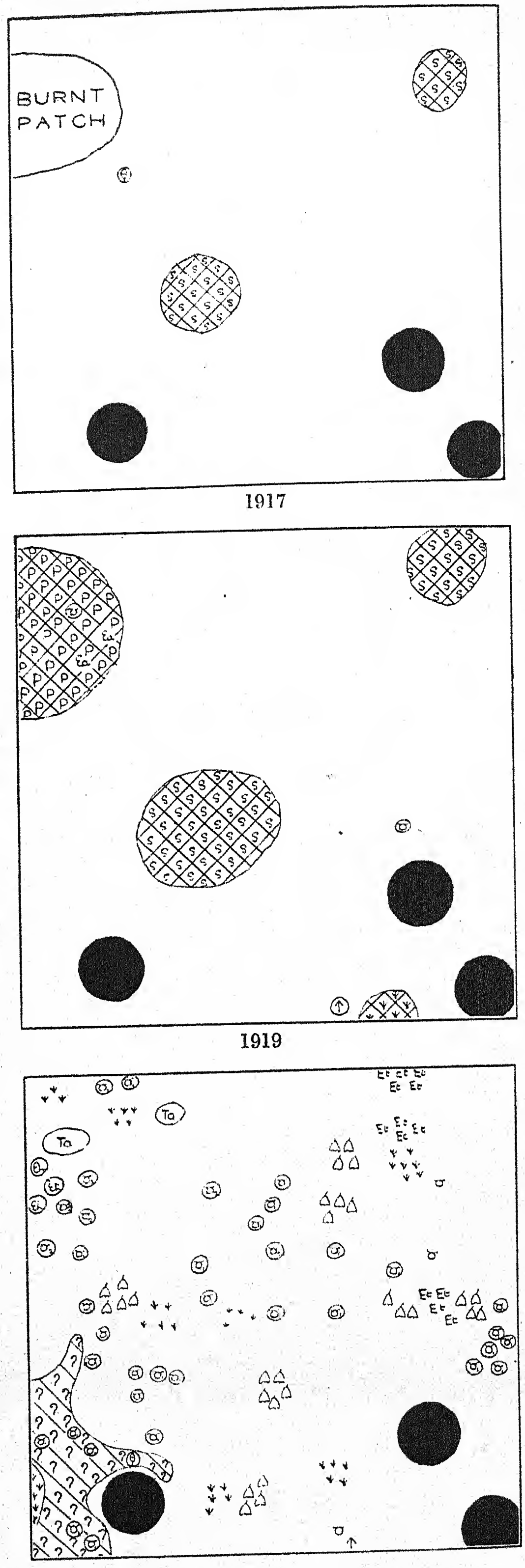

Fig. 6. Charts of quadrat 14 (20 × 20 ft.) in the same years, illustrating the establishment of birches, *Betula alba* (*verrucosa*) and *B. pubescens*.

For key to symbols see page 129.

lopus was further destroyed, and by the end of the year a large central region of the observational area was again bare of vegetation. A deep hole dug in the south-west corner on June 10th had revealed no water even at a depth of three-and-a-half feet, though the sand became moist to the spade at a depth of nearly three feet.

It was evident in the autumn, that seedlings of *E. tetralix,* which had appeared among the *Molinia* plants in the north-east corner, were less affected by the drought than was *Molinia* itself. The rabbits had left the *Calluna* for the more succulent young birches and had nibbled leaves and dragged off the twigs up to a height of two or more feet. The bracken rhizomes on the oases were unable to continue their underground growth. In some cases the apex was still alive, in others it had perished but was still fixed in the ground, and where the apex had failed to progress, knee-like ascending curves were formed by the rhizomes in their growth (Fig. 4). It seemed that elongation of the rhizome had been taking place but not at the apex. To verify this a detailed map of one oasis made in May of that year was compared with the oasis in its autumn state, and a record was made of the change in extent of the bracken in the five months that had elapsed. It was found that not only was the extent reduced along many radii, but there had been no considerable addition along any radius.

Very little progress was made therefore in 1921 owing to the fire in January and the subsequent drought, which not only retarded but actually destroyed much of the early beginnings of growth. Indirectly these events caused the destruction of the lower branches of many birches, as the heather became too dry to be palatable to rabbits. During the following winter the rabbits did further injury to heather and birches and to the bracken, not only in its subterranean parts but in the newly exposed parts of the rhizomes (see Fig. 4).

A comparison with a neighbouring lumbered pinewood, viz. Callow Hill, was made in July. Here the vegetation had advanced much more rapidly. Nearly the whole hill side was covered with bracken, and there was much *Vaccinium myrtillus* and several young deciduous trees: *Rhamnus frangula, Quercus* sp. and *Castanea.* Oases which, three years previously, had been as

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KEY TO FIGURES 5, 6, 7 AND 8.

	OLD PINE STUMP		MOLINIA CAERULEA
	BETULA ALBA		PTERIDIUM AQUILINUM
R	RHODODENDRON PONTICUM		SPHAGNUM spp.
	QUERCUS ROBUR (PEDUNCULATA)	P	POLYTRICHUM COMMUNE
	ULEX EUROPAEUS	Di	DICRANUM LONGEANUM
	SEEDLING PINE, ULEX, BIRCH AND OAK	ııı D ııı	DESCHAMPSIA FLEXUOSA
Ec	ERICA CINEREA	Ta	TARAXACUM VULGARE
	ERICA TETRALIX	Ea	EPILOBIUM ANGUSTIFOLIUM
	CALLUNA VULGARIS	Eh	EPILOBIUM HIRSUTUM

well delimited as those on the Virginia Water area, were no longer distinguishable from the surrounding land, which was carpeted with vegetation. Another neighbouring lumbered area, viz. the Clockcase Woods, was still covered in many parts with an almost pure growth of *Epilobium angustifolium.* Thus three areas once dominated by *Pinus sylvestris* were regenerating along different lines.

OBSERVATIONS MADE DURING 1922

As already stated, the *Campylopus* covering of the central and otherwise barren area had been destroyed by the drought in 1921. It was interesting therefore to note in January 1922 that the soil had become almost covered with lichens, chiefly *Cladonia* species and some *Peltigera.* A careful examination of the soil for the presence of earthworms was made but no trace of worms or their casts was found, even in the vicinity of the bordering paths.

The exceptionally hot early summer was followed by a cool and rainy season which was extraordinarily favourable to the regeneration of the area. The ripening of spores and seeds served further to promote it. The history of the selected oasis was continued. The records made in October showed that the rhizomes of the bracken now extended from the centre of the oasis to a distance of $14\frac{1}{2}$ feet. This indicates the favourable conditions for growth of bracken that prevailed during the latter part of the summer of 1922.

When 1922 closed the observational area looked quite overgrown and it was difficult to see the boundary. The tallest birches were six feet in height. There was still a considerable barren area in the centre: even the lichens which covered it in January had withered during the heat of the early summer.

The same rapid regeneration of the vegetation was observed in the two other lumbered areas during repeated visits made throughout the year. The development of their vegetation in 1922 accentuated the differences between them—differences not only floristic but also distributional. By means of contour maps the distribution of vegetation in all these areas was compared. From these it became evident that the inclined surface was always better populated than the flat surface above it, and less well populated than the flat surface below it, and this irrespective of aspect. It would appear either that the leaching of the plateau by rain was unfavourable to the establishment of new vegetation, or that the plateau periodically became too dry to support plant life.

OBSERVATIONS MADE DURING 1923 AND 1924

In 1923 no records were made beyond the listing of plants that occurred in that year and the measuring of the bracken colonies.

By 1924 the observational area was already a young birch wood (Fig. 6). The birches numbered some thousands and many had attained a height of 10 feet and more. There was still a bare region in the middle. Elsewhere the ground was covered with vegetation.

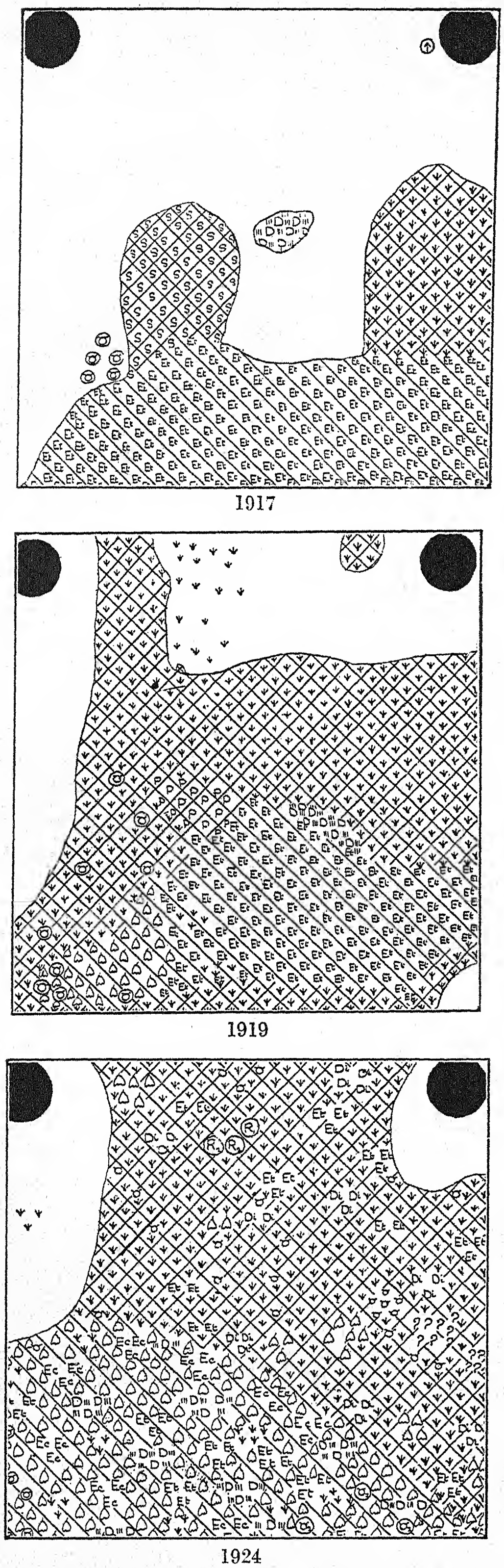

Fig. 7. Charts of quadrat 4 (20 × 20 ft.) in the years 1917, 1919 and 1924, illustrating the invasion by *Calluna vulgaris* of the already established *Erica tetralix*.

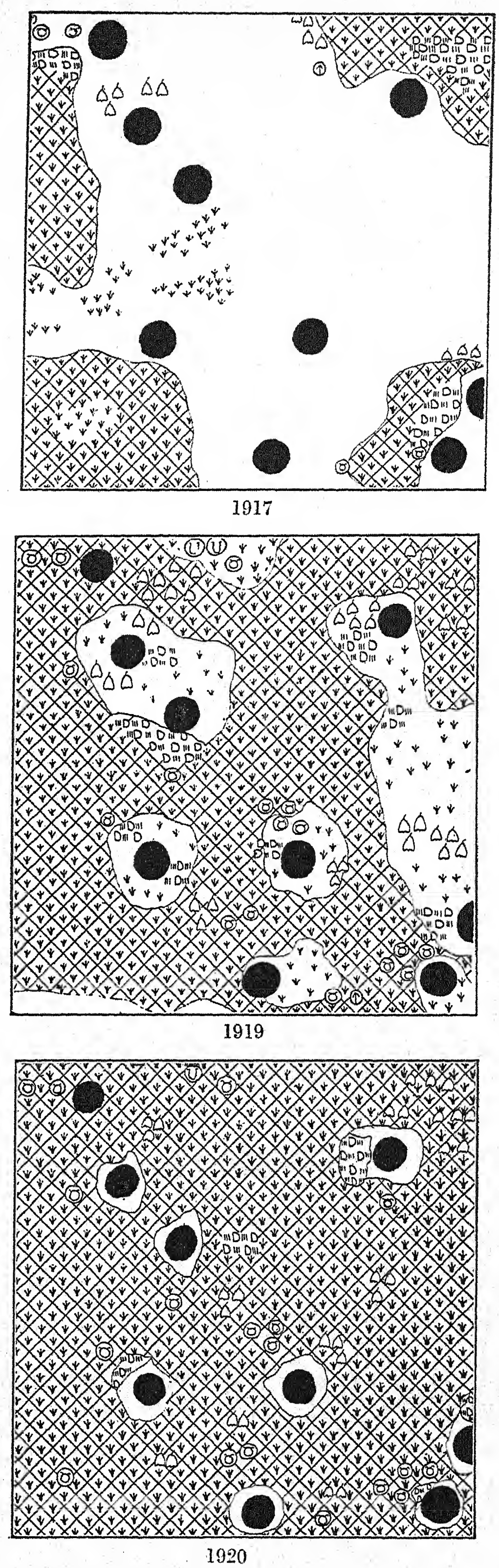

Fig. 8. Charts of quadrat 39 (60 × 60 ft.) in the years 1917, 1919, 1920, showing the spread of *Molinia*.

For key to symbols see page 129.

Molinia caerulea and heaths, of which *Erica tetralix* was more abundant than *Calluna vulgaris*, were dominant and *Pteridium aquilinum* was locally dominant. There was no doubt that the steady progression of *Pteridium aquilinum* still continued. On the other hand *Calluna vulgaris* and *Erica tetralix* had often given way before encroaching *Molinia*. To a casual observer the grasses were the most noticeable feature of the ground flora, but in February 1925, when the birches and taller herbs were cut down by the forest authorities of Windsor Great Park, the equal dominance of the heaths was obvious.

Of the less frequently occurring members of the community, special mention must be made of young pines and rhododendrons, which occurred sporadically in the moister parts, that is along the ditch and near the bog. Twenty saplings of *Pinus sylvestris* and 103 seedlings of *Rhododendron ponticum* were counted. These numbers are explained by the fact that there were in the neighbourhood many rhododendron shrubs and a pine tree.

Other colonists recorded are:

ANGIOSPERMAE.

Quercus robur (pedunculata)	12	Deschampsia flexuosa	occ.
Ulex europaeus	6	Taraxacum vulgare	occ.
Ilex aquifolium	1	Urtica dioica	2
Rhamnus frangula	5	Rumex acetosella	2
Rubus fruticosus	2	Juncus communis	occ.
Erica cinerea	occ.	J. bulbosus	
Epilobium hirsutum	occ.	(=J. supinus, Moench)	1

BRYOPHYTA.

Sphagnum Polytrichum Dicranum

Old stumps of trees were found to be covered with lichens, e.g. *Parmelia fuliginosa* var. *laetevirens* and *Physcia ciliaris*, and mosses, e.g. *Hypnum cupressiforme* and *Ceratodon purpureus*.

The bare central region, which was higher than the rest and covered with a thin humus of pine needles, was colonised almost entirely by lichens and mosses which formed a close covering. *Cladonia maculenta*, *C. fimbriata* and occasionally *Peltigera canina* were found, and *Campylopus pyriformis* was frequent. Very rarely there occurred closely nibbled plants of *Calluna vulgaris*, and the less high regions around were sparsely covered with partly nibbled *Molinia caerulea*, untouched *Erica tetralix* and occasional *Festuca rubra*.

In order to discover how far the bareness of the central region was due to the ravages of rabbits, wire cages were set up in June 1924, each enclosing a square metre of ground; but no definite conclusions could be drawn from observation of these for they were unexpectedly destroyed six months later. In January 1925 the forest authorities of Windsor Great Park cut down the natural birchwood that had established itself on the observational area and replanted *Pinus sylvestris*.

LIST OF PLANTS RECORDED DURING 1917–1925

DICOTYLEDONS.

Betula alba (verrucosa)
B. pubescens
Calluna vulgaris
Castanea sativa
Cuscuta epithymum
Epilobium angustifolium
E. hirsutum
Erica cinerea
E. tetralix
Ilex aquifolium
Potentilla erecta
Quercus robur (pedunculata)
Rhamnus frangula
Rhododendron ponticum
Rubus fruticosus
Rumex acetosella
Salix sp.
Senecio vulgaris
Taraxacum vulgare
Ulex europaeus
Urtica dioica

MONOCOTYLEDONS.

Deschampsia flexuosa
Festuca ovina
F. rubra
Juncus bulbosus
J. communis
Molinia caerulea

GYMNOSPERMS.

Larix europaea
Pinus sylvestris

PTERIDOPHYTA.

Pteridium aquilinum

BRYOPHYTA.

Marchantia polymorpha
Barbula fallax
Campylopus flexuosus
C. pyriformis
Ceratodon purpureus
Dicranum longeanum
Funaria hygrometrica
Hypnum cupressiforme
H. purum
Leucobryum glaucum
Mnium sp.
Polytrichum commune
Sphagnum spp.

FUNGI.

Bulgaria polymorpha
Calocera cornea
Claviceps purpurea
Flammula sapinea
Galera hypnorum
Hypholoma fastigiata
Laccaria laccata
Merulius tremulosa
Mycena epipterigia
Paxillus involutus
Scleroderma vulgare

together with various species of Phycomycetes and Myxomycetes.

LICHENS.

Cladonia fimbriata
C. maculenta
Peltigera canina
Parmelia fuliginosa
Physcia ciliaris

ALGAE.

Since 1919, a certain number of soil algae have been isolated, of which *Cystococcus* is the most frequent unicellular form and *Hormidium* the dominant filamentous. Perhaps the most interesting feature is the extraordinary abundance of *Carteria* from 1923 onwards, in the surface soil of the wetter parts.

DISCUSSION

The plant succession on the area passed through various stages of heath towards the establishment of a dense young birch-wood. In the centre of the

area even to the last (1925) there remained a bare region. The marked failure of all plants other than *Cladonia* spp. and *Campylopus* spp. to colonise here was striking. It could not be that seeds and spores did not arrive. It was at first attributed to the ravages of rabbits, but the isolation of a portion of the ground by means of cages of wire-netting did not, in the short period over which observations were made, justify this conclusion[1]. The ground was higher here and its bareness may have been due to special conditions of leaching by rain or of extreme drought. The latter condition existed for short periods during the summer months, when the water table was very low. Possibly the area did not remain sufficiently moist for long enough at a time to allow seedlings and sporelings to become established. In addition to the lichen and moss mentioned above only occasional plants of *Calluna vulgaris* managed to get a hold; these were nibbled close by rabbits.

The failure of the pines to re-establish themselves may have been due, at least in part, to the attacks of the weevil which, by 1920, had become abundant among the pine stools. It is well known that weevils feed on young pines, and some pines had been attacked. No traces were ever found of the pine beetle (*Hylesmus piniperda*, L.), and this was due undoubtedly to the preliminary burning of the tree tops by the lumbermen. Apart from the weevil, disease and competition appear to have but little affected the vegetation, although ergot (*Claviceps purpurea*) occurred on *Molinia*, and dodder (*Cuscuta epithymum*) on *Calluna*. As natural regeneration of pines on the moister regions of the Bagshot Sands is known to occur, however, further explanation should perhaps be sought for their failure in this region. No less than 55 pine seedlings were counted in 1917, and 62 in 1919, but only 20 in 1924. These 20 surviving pines were all in the peripheral region of the area, on ground which had never been burnt or otherwise completely denuded. Fourteen of them are marked on the maps for 1917, 18 on the maps for 1919, and it is possible that the other two were overlooked. In 1925 they were well grown trees of 3 to 4 feet in height. Pine seedlings have rarely established themselves since the area was lumbered. It is evident that the ground is suitable for pines once they have established themselves, for the area has been successfully replanted with pines and was, of course, previously a pine-wood. Many suggestions might be offered to account for the failure: e.g. the possible loss by fire or drought of the essential symbiotic fungus of the roots, or the special character of coniferous wood, or the shallow root system of pine seedlings which could not withstand the periods of drought. Up to 1920 *Molinia* and *Betula* were the two Phanerogamic species which were best established on the area. The heaths had obtained a hold, but were not so abundant as *Molinia* and *Betula*.

In order to discover what characteristic of these plants made them more successful than any other colonists the root systems were compared with

[1] See note on page 137.

those of other species occurring on the area. It was found that two year old pine seedlings, *Erica*, *Calluna*, and *Deschampsia*, had root systems which ramified profusely in the humus, but did not penetrate the sand. In the case of two year old birches and *Molinia*, however, the roots reached the water level. These two species therefore were more capable of withstanding periods of drought, than were the shallow rooted plants. The establishment of the heaths on the area, in spite of their roots not tapping the water table, causes no surprise, for it is well known that the xerophytic character of their leaves enables the plants to thrive in difficult conditions of water supply. It is possible that the leaves of seedling pines are not so well equipped.

In the ravages caused by rabbits it is certain that *Calluna vulgaris* suffered most. *Erica cinerea*, *Molinia caerulea*, and *Deschampsia flexuosa* were often nibbled and in 1921, during the great drought, the rabbits left the dry *Calluna* for the more succulent young birch trees. *Erica tetralix* on the other hand was absolutely untouched. The preference shown by rabbits for *Calluna vulgaris* was very marked. This preference was an independent observation during the course of this work. We have since noted with interest that Farrow, in his work on the vegetation of Breckland (This JOURNAL, **5**), has observed the same thing. In some parts, however, in spite of this, *Calluna vulgaris* steadily invaded the already established *Erica tetralix* (Fig. 7).

Among the problems which interested us was the scarcity of the Rose bay willow-herb (*Epilobium angustifolium*). The fact that only two flowering specimens of "Rose bay," or as the Canadians call it, on account of its presence after forest fires, "Fire weed," have ever been observed on the plot, has caused surprise. Its complete failure to establish itself is especially interesting on account of its wide occurrence on a similar lumbered region, called the Clockcase Woods, about a quarter of a mile distant on the south side of the Bagshot road. Rose bay grows abundantly on this land, and is spreading vegetatively, and by seed. The Clockcase Woods are on higher ground than the observational plot, and also on a steeper slope. The water table in the Clockcase Woods was 4 ft. 3 ins. below the surface, as compared with 20–30 inches in the Virginia Water area, when measured in November 1920. This level coincided with the level of the surface of the clay in the latter area, but, at a depth of 4½ feet, no clay was found in the Clockcase Woods. Probably these differences unite to ensure in the soil of the Clockcase Woods a better drainage system, and more efficient aëration and nitrification than are found in that of the Virginia Water area. The Swedish botanists regard the Rose bay as a good index of active nitrification in forest soils. It is suggested that these factors may account for Rose bay occurring so abundantly in the Clockcase Woods, and so rarely in the other area.

With reference to the record of *Marchantia*, we may note that, while *Lunularia* and *Pellia* are extraordinarily abundant in the near neighbourhood of the College, *Marchantia* has always been scarce, and no member of the

College has known it to fruit in this district. The sudden appearance on the area of plants which were fruiting so abundantly that the ground was yellow with the shed spores caused, therefore, no little surprise. But the arrival of the plant was hardly more extraordinary than its almost total disappearance after two years of apparently successful establishment. The latter phenomenon may perhaps be partly accounted for by the sharp competition which occurred on the oases.

The sudden appearance of *Bulgaria polymorpha* in 1917 was not so surprising, for it is a common fungus in the neighbourhood. Its enormous size and its abrupt and complete disappearance were, however, most remarkable. It has not been recorded for the area since 1918.

SUMMARY

1. An account is given of the colonisation of a denuded area, the observation of which extended over eight years, viz. from the complete destruction by felling of a pine-wood in 1916, to the destruction in 1925 of a young birch-wood which had established itself in its place.

2. The establishment of a birch-wood on the waste ground of a destroyed pine-wood was due to two factors:

(*a*) The failure of *Pinus sylvestris* to re-colonise the ground: pine seedlings numbered 55 in 1917, 62 in 1919 and 20 in 1924.

(*b*) The immense success of *Betula alba* both in growth of each individual (many had attained ten feet in height by 1925), and its quick increase in number (birch seedlings numbered 53 in 1917, 219 in 1919 and over 1000 in 1924).

3. In the record by notes and maps made from year to year of the evolution of the birch-wood further facts of general interest made themselves evident:

(*a*) The immediate colonisation of certain burnt patches of ground by *Marchantia polymorpha* and *Funaria hygrometrica*.

(*b*) The establishment of *Pteridium aquilinum* in these moist nests of Bryophyta.

(*c*) The steady advance of the *Pteridium* from these definite centres over the surrounding, usually bare, ground.

(*d*) The widespread colonisation of the area by numerous individuals of *Betula alba, Molinia caerulea, Erica tetralix* and *Calluna vulgaris*.

(*e*) The competition between *Molinia* and the heaths, which, to the casual observer in 1924, appeared to be won by *Molinia*, although, as was clearly seen after the cutting down of the vegetation in 1925, neither could be considered dominant.

(*f*) The competition between *Calluna vulgaris* and *Erica tetralix*, in which the latter became dominant on the moist parts and the former on the high and dry parts; in which too the latter had an advantage in being distinctly more successful in the early years.

(*g*) The obvious preference shown by rabbits for the *Calluna*.

(*h*) The striking absence of angiosperms other than the few mentioned above, especially of *Epilobium angustifolium*, which in other regions was locally dominant in similar denuded and burnt areas.

4. Certain facts of special interest emerged:

(*a*) The outcrop of immense sporophores of *Bulgaria polymorpha* in the first two years, and its total absence since 1918, although other fungi, lichens and mycetozoa were numerous on the ground and on the old tree stumps.

(*b*) The luxuriance of *Marchantia polymorpha* in 1919, especially rich in archegoniophores, antheridiophores, and gemmae, and its total disappearance later, along with its fellow pioneer *Funaria hygrometrica*.

(*c*) The special method of dispersal of the moss *Campylopus flexuosus*, which ensured its widespread success until the drought in 1921.

(*d*) The peculiar knee-like curves of the lengthening rhizomes of *Pteridium aquilinum*, whose growing points were prevented from advancing in the hard ground after the drought in 1921.

Acknowledgments are due to our colleagues N. Thomas (Mrs Ferguson) 1917–1919, and K. E. Light 1919–1925, and to students in the Botany School, Royal Holloway College, during the years 1917–1925. The figures have been drawn by M. I. Thomas.

NOTE ADDED JANUARY, 1926.

It is now possible to make a more definite statement with regard to the influence of rabbits on the bare central region.

Before replanting with pines in January, 1925, the forest authorities enclosed the whole area by rabbit-proof fencing. In the autumn of that year it was observed that the central region was becoming colonised to some degree. The occasional old plants of *Calluna vulgaris* were no longer closely nibbled and new plants had established themselves. Photographs taken from the same spot in June, 1924, and October, 1925, show a noticeable increase in vegetation in the central region. Destruction by rabbits, therefore, was *one* factor responsible for the continued failure of vegetation to colonise the central region during the eight years the area was under observation.

ON THE ORIGIN OF THE XEROTHERMIC PLANT ELEMENT IN BULGARIA

By N. STOYANOFF.

The vegetation of Bulgaria has been often described as being of a steppe character. Such terminology may be found both in descriptions by well-known travellers and in contemporaneous geographical manuals. Although partly exaggerated these descriptions correspond to a certain extent with the opinion of several phytogeographers. Thus, Velenovsky[1] describes as a steppe the environs of Rahovo and Burgas, and Podpera[2] those of Khaskovo. However, after studying carefully the vegetation of such woodless localities in Bulgaria, it becomes evident that this steppe character is hardly natural. Even in such especially treeless districts as the environs of Gebedje in eastern Bulgaria, numerous remnants of a former forest vegetation may be observed in the form of reduced shrubs of *Quercus pubescens, Ulmus campestris, Carpinus duinensis, Fraxinus ornus, Acer campestre*, etc. Here and there even separate small trees are yet preserved. In the above mentioned localities near Rahovo, Burgas and Khaskovo such remnants of a former forest vegetation are rather more evident. The country between Sofia and Dragoman, which Lavelyé[3] describes as a real steppe, was covered in historic times with large forests, which formed a part of the famous *Sylva bulgarica*, renowned in the history of the Crusades. Remnants of the forest vegetation, which composed these woods, are even comparatively abundant to-day. The forests of Deli-Orman in north-eastern Bulgaria are the last remains of the natural vegetation, which once covered the now nearly woodless plain of the Danube.

The present lack of trees and the spreading of the steppe plants in many parts of Bulgaria are chiefly due to the direct and indirect activities of man. Adamovič[4] gives a true and instructive description of how wooded areas in Bulgaria and the neighbouring countries are gradually transformed into scrub-land by man and his methods of farming. Afterwards the bushes disappear also and the terrain becomes like a real steppe.

The plants, spreading through such deforested terrains, belong mostly to xerothermic species, such as are able to spread rapidly and to accommodate themselves easily to new conditions. Their dispersal is indirectly aided by man,

[1] **J. Velenovsky.** *Flora bulgarica. Suppl.* **1**, 324–327.

[2] **J. Podpera.** "Ein Beitrag zu den Vegetationsverhältnissen in Südbulgarien." *Verhandl. d. zool.-bot. Ges.* p. 608. Wien, 1902.

[3] **E. de Lavelyé.** *La péninsule des Balkans*, pp. 56–58. Bruxelles, 1886.

[4] **L. Adamovič.** *Die Vegetationsverhältnisse der Balkanländer*, pp. 526–528. Leipzig, 1909.

and increases with the enlargement of the cultivated surface. Many of them belong to the ruderal and half-ruderal element.

Representatives of such a secondary steppe vegetation are:

Andropogon ischaemum
A. gryllus
Cynodon dactylon
Poa bulbosa
Bromus erectus
Festuca ovina
Aegylops cylindrica
Carex praecox
Polygonum convolvulus
Silene otites
Stellaria graminea
Cerastium arvense
Holosteum umbellatum
Herniaria glabra
H. hirsuta
Sanguisorba minor
Potentilla recta
P. argentea
P. canescens
Medicago falcata
M. minima
Melilotus officinalis
Astragalus onobrychis
Coronilla varia
Linum perenne
Polygala comosa
Euphorbia virgata
E. gerardiana
Eryngium campestre
Bupleurum falcatum
Falcaria rivini
Nonnea pulla
Onosma spp.
Ajuga genevensis
A. laxmanni
Teucrium polium
Salvia silvestris
S. aethiopis
Stachys germanica
S. recta
Verbascum spp.
Linaria genistaefolia
Veronica spicata
V. teucrium
V. chamaedrys
Plantago lanceolata
P. arenaria
Asperula cynanchica
A. galioides
Galium verum
Scabiosa ucranica
S. ochroleuca
Campanula trachelium
C. bononiensis
Achillea millefolium
A. setacea
Artemisia campestris
Centaurea spp.
Tragopogon majus
T. orientalis
Lagoseris bifida, etc.

In some parts of South Bulgaria, as for example around Khaskovo, the presence of numerous Papilionaceae and among them especially of different species of *Trifolium* is characteristic for such pseudo-steppe formations. A similar spreading of the xerothermic elements, due to the activities of man, has been observed also in other countries of Europe. It is noted in the Western Alps by Briquet[1], in Germany by Weber[2] and Schalow[3], etc.

Simultaneously with this secondary steppe vegetation traces of a primeval xerothermic plant element may be observed in Bulgaria. It differs from the above described in several respects. It is neither able to spread extensively, nor to accommodate itself to any new ecological conditions created by man. Its components are therefore generally distinguished by their conservative character and may be met here and there in localities which are little influenced by cultivation and probably were not wooded even in those times when Bulgaria was more forested than it is to-day. Refuges or relict-places of such plants may be chiefly found on dry limestone rocks, less often on other kinds of dry rocks, on sand, salty soils, etc. Such a characteristic refuge may be observed on the rocky limestone hills between Dragoman and Belidie in Western Bulgaria. On these hills there are growing:

Stipa pennata
Agropyrum cristatum
Allium saxatile
Silene longiflora
Anemone silvestris
Potentilla rupestris
Amygdalus nana
Astragalus testiculatus
A. depressus
A. pubiflorus
Anthyllis montana
Cachrys alpina
Eryngium palmatum
Hyssopus officinalis
Goniolimon tataricum
Artemisia camphorata
Jurinea tsar-ferdinandi, etc.

[1] **J. Briquet.** "Le développement des Flores dans les Alpes occidentales." *Résult. scient. du Congrès Internat. Botan.* pp. 166–167. Vienne, 1905.

[2] **A. Weber.** "Die Geschichte der Pflanzenwelt des norddeutschen Tieflandes seit der Tertiärzeit." *Ibid.* p. 111.

[3] **E. Schalow.** "Die Pflanzenverbreitung und vorgeschichtliche Besiedelung." *Naturwiss. Wochenschr.* pp. 173–177, 1922.

Another similar oasis with evidently old xerothermic vegetation lies on the limestone rocks and calcareous sands near Gebedje, in Eastern Bulgaria. Of the xerothermic plants, which occur there, may be mentioned:

Silene supina	Lepidotrichum uechtritzianum	Hedysarum tauricum
Gypsophila paniculata	Astragalus virgatus	Ruta biebersteinii
Arenaria rigida	A. austriacus	Matthiola tristis
Thymus carnosulus	A. vesicarius	Salvia grandiflora, etc.
Linum flavum	A. albicaulis	

Refuges of conservative xerothermic plants may be observed also in many localities, spread almost over the whole surface of Bulgaria. As representatives of this type of vegetation the following species may be listed:

Ephedra vulgaris	Saponaria bellidifolia	Anthyllis aurea
Stipa aristella	Queria hispanica	Polygala supina
S. capillata	Minuartia montana	P. rhodopea
Bromus transsilvanicus	Iberis saxatilis	Pimpinella tragium
Brachypodium sanctum	Spiraea crenata	Androsace maxima
Psilurus nardoides	Caragana frutescens	Verbascum humile
Lepturus pannonicus	Astragalus physocalyx	Celsia orientalis
Sternbergia colchiciflora	A. pugioniferus	C. roripifolia
Asphodeline taurica	A. thracicus	C. rupestris
Allium flavum	A. jankae	C. bugulifolia
Silene chlorantha	A. arnacantha	Morina persica, etc.

A recent extension of most of the above xerothermic plants can hardly be postulated. Most of them cannot withstand the influence of cultivation, and disappear in localities to which farming extends. Practically none of them shows any tendency to increase the area of its distribution in Bulgaria, at least under the present physical conditions. Some of them show features characteristic of relict organisms, whilst they do not reproduce freely. Some of them even seem to be on the way to extinction in Bulgaria. *Astragalus physocalyx*, an old type, belonging to the monotypic Section *Pogonotropis*, is a good example. The only place, where this plant was known to grow, was on a rocky hill near Philippopel. Even in 1871 Janka, after a long search, could find only a single group of 10 specimens of this plant[1]. He stated then, that only a few of the fruits he found on these plants seemed to produce viable seed. During the last 17 years *Astragalus physocalyx* has not been found, either in that place or elsewhere, and the only two living specimens, known at present, are growing in pots in the Royal Botanic Garden in Sofia. All attempts to multiply this species were unsuccessful, because ripe fruits of it can be rarely obtained. *Jurinea tsar-ferdinandi*, growing on the limestone rocks near Dragoman, does not seem to flower every year, and even when it does, the flowers and fruits are usually not abundant. *Astragalus testiculatus*, which also grows near Dragoman, seems similarly to have only slight powers of reproduction.

Many of the plants listed above have a limited distribution in Bulgaria,

[1] **V. Janka.** "Correspondenz aus Philippopel" in *Oesterr. bot. Zeitschr.* p. 218, 1871.

being known only in one or two isolated localities. Thus *Cachrys alpina*, *Astragalus testiculatus*, *Paeonia corallina* and *Artemisia chamaemelifolia* are each known from only one locality in Western Bulgaria, *Iberis saxatilis*, *Astragalus arnacantha* and *A. jankae* each from one locality in Southern Bulgaria, *A. pubiflorus* in two isolated places in Western and Eastern Bulgaria, *Alsine montana* in one place in Bulgarian Macedonia. *Brachypodium sanctum*, *Asphodeline taurica*, *Polygala supina*, *Verbascum humile*, etc. are growing in discontinuous and isolated areas.

The existence of relict xerothermic plants, which may be found in several isolated places, dispersed over almost the whole surface of Bulgaria, supports the opinion, that Bulgaria has passed through an era of time when xerothermic plants were more widely spread than they are at present and when the climate was relatively drier. That era probably corresponds with the period when in Northern Bulgaria the thick layers of loess were formed, which are so characteristic of this part of the country. It was probably the time which is described by geologists for Middle Europe as the Aquilonar or Steppe period.

A similar twice repeated spreading of the steppe vegetation has been observed also in neighbouring countries. Thus in Southern Russia, according to Kusnezow[1], the steppe vegetation has enlarged its area within historic times, in consequence of the destruction of forests by man. In prehistoric times the forests had advanced southwards over the steppe. However, traces are found also of an old wider spreading of steppes, which preceded the natural extension of forests in Southern Russia.

In that more remote period there probably occurred in Bulgaria the extensive development of certain plant genera such as *Genista*, *Astragalus*, *Verbascum*, *Centaurea* and certain sections of *Dianthus*, which are now represented by numerous species. Some of them seem to have continued this development till the present time; some others, such as *Verbascum*, are now represented by mostly constant and well limited forms.

If we examine the geographical distribution of this xerothermic vegetation, it becomes evident that it has a considerable and direct connection with the steppe vegetation of Southern Russia. How intimate this connection is may be illustrated by the fact, that of 425 species, which Krasnov[2] refers to as characteristic of the South-Russian steppes, 272, i.e. more than 60 per cent., occur also in Bulgaria. Besides this there is a noteworthy connection also with the Mediterranean flora, as has been observed by all investigators of the Bulgarian flora.

In many cases xerothermic plants are so widely spread both in the Mediter-

[1] **N. J. Kusnezow.** "Die Vegetation und die Gewässer des Europäischen Russlands" in *Engler's bot. Jahrb.* Bd. **28**, 221–222, 1899–1901.

[2] **A. Krasnov.** "Steppes de la Russie méridionale." *Annales de géographie*, **111**, 315–318, 1894.

ranean and the Steppe provinces, that it is difficult to decide to which group they may belong. As examples may be mentioned:

Stipa pennata	Salvia aethiopis	Triticum cristatum
S. capillata	Scutellaria orientalis	Ephedra vulgaris
Phleum boehmeri	Chondrilla juncea	Asparagus officinalis
Crypsis alopecuroides	Erysimum repandum	Allium moschatum
Euphorbia gerardiana	Eryngium campestre	A. flavum
Teucrium polium	Androsace maxima	A. paniculatum, etc.

The South-Russian steppes, whose vegetation is so closely related to the Bulgarian xerothermic plant elements, are a relatively new formation, geologically speaking. Their flora is consequently also of a relatively new origin and received its elements from the neighbouring countries, after the recession of the sea, which formerly covered that province.

Only a very small proportion of the steppe plants can be supposed to have originated in Southern Russia itself. Krasnov mentions 16 species, which he supposes to be endemic and original elements of that vegetation. These plants are growing in the most elevated parts of the South-Russian steppes, on areas of soil which, according to the Russian geologists, have not been covered with water, but formed islands in the Quaternary South Russian Sea. This statement of Krasnov's received lately an indirect affirmation by Kuzniar's investigations[1]. This author found in Southern Russia traces of an old mountain range, which ran in the direction—from Volhynia and Podolia, across Jitomir and Ekaterinoslav towards the estuary of the Don. This mountain range was connected by extensions with the Crimea and Caucasus and also with the Dobruja, i.e. with the eastern part of the Balkan Peninsula. Szafer[2] records Tertiary relict plants in the vegetation of Volhynia and Podolia, whose presence is connected with the history of that mountain range. It is therefore interesting that of the 16 species mentioned by Krasnov as relicts, one is related to a species known from the Balkan Peninsula and one is recorded from Bulgaria. *Schiwereckia podolica* is represented in the mountains of the Balkan Peninsula by a closely related species—*S. bornmulleri*, while *Asperula tyraica* is recorded from Bulgaria.

South Russia is, from the geographical point of view, only an advanced post of the large steppes and deserts of Western and Central Asia, hence the closest relationship between the vegetation of these countries is to be expected. Such relationship is accepted as a matter of course by many floristic investigators. An especial light is thrown on the character of this relationship by the conclusions reached by Borszczow[3], whose knowledge of the steppe vegetation in European and Asiatic Russia is above all doubt. These conclusions are summarized by him in the following six points:

(1) The majority of the commoner plants of Central Russia with a distribution west of the Caspian Sea, extending to Transcaucasia, have as their

[1] According to **W. Szafer:** "Les plantes tertiaires montagnardes sur la chaîne scytique dans le refuge de Podolie et Volhynie." *Acta Societ. botan. Poloniae*, **1**, 97–119, 1923.

[2] *L.c.*

[3] See **O. Paulsen** cited below.

southern limit of distribution east of the Caspian Sea in Aralo-Caspia, the parallel of $51\frac{1}{2}°$ N. lat.

(2) When these forms occur farther east in Siberia, the boundary limiting their area of uninterrupted distribution lies outside of Aralo-Caspia and always north of $51\frac{1}{2}°$ N. lat.

(3) *Most of the typical steppe plants met with in Southern Russia, and distributed towards the west from the Caspian to the foot of the Caucasus, attain their southern limit in Aralo-Caspia at the parallel of 49° N. lat. and their eastern boundary at the meridian of the Mugodshar range; if they occur farther east, they never go farther south than 49° N. lat.*

(4) The more southern plant forms, characteristic both for Persia and Aralo-Caspia, do not occur in our flora of the present time farther north than 49° N. lat.

(5) The more eastern forms, met with in the Altaian Siberia, are rarely met with farther west than 78° E. long. F. (about 60° E. Greenwich).

(6) In the case of a great many south-eastern forms, the lower course of the Syr-Daria (45–46° N. lat.) is the northern boundary and the meridian of the eastern shore of the Aral Sea (70° E. long. F.—about 62° E. Greenwich) forms the western boundary[1].

If we trace on a geographical map the boundaries mentioned by Borszczow, becomes evident, (1) that the steppe flora in South-Eastern Europe has relatively little in common with the xerophytic vegetation of Turkestan and Central Asia; (2) that a flora, related to that of the steppes in South-Eastern Europe, occurs in Western Siberia only in a tract of land which lies between 49° N. lat. and the belt of the Siberian forests. These facts scarcely harmonize with the common conception of the South-Eastern European steppes as only a branch of the large steppes and deserts of Asia. However, almost the same conclusions have been reached by modern Russian botanists. Thus according to Kuznezov[2], the steppes of Western Siberia occupy a tract of land, whose northern boundary runs across Jalutorovsk, Ishim, Tatarskaia, Kolivan, then makes a bend at the foot of Altai, across Kusnetsk, Biisk, Lokotievsk, takes a direction towards the south-east, along Irtish and the Lake Zaisan-Nor and reaches Western Mongolia. Their southern boundary lies on the watershed between the Arctic Ocean and the Aralo-Caspian basin. South of this watershed are spread the steppes and deserts of Turkestan, whose vegetation belongs, according to Korzinsky, to another type, namely to a southern or subtropical flora.

It is difficult to say what kind of historical relationship exists between the steppe flora of South-Eastern Europe and that of the above described relatively

[1] According to **O. Paulsen.** "The Second Danish Pamir Expedition, conducted by O. Olufsen." *Studies on the Vegetation of the Transcaspian Lowlands*, pp. 29–30. Copenhagen, 1912.

[2] **N. J. Kuznezov.** "Essai d'une division de la Sibérie en provinces phyto-géographiques." *Bulletin de l'Acad. Imp. des Sciences de St. Pétersbourg*, pp. 894–895, 1912.

narrow tract of land in Western Siberia. The few geological facts known about Western Siberia give no clear answer to this question. However, there are few grounds for supposing that a centre of development for xerothermic vegetation lay in that part of Siberia. According to the geological investigations, the Caspian Sea was connected with the Arctic Ocean even to the beginning of the Glacial period. Published opinions are contradictory as to whether this connection was across Western Siberia or across the eastern part of European Russia. Most of the geologists agree that large water basins occupied Western Siberia, north of the watershed between the Arctic and the Aralo-Caspian, up to the beginning of Post-glacial times. Even at present small water basins are extremely abundant over the whole of the West-Siberian steppes. More than 200 lakes may be seen within the limits which Kuznezov traced for these steppes, by examining even a relatively small map of Asia[1]. There is no doubt that these water basins formerly had a notably larger extent than they have to-day. Thus Krilov[2] proves that a large lake existed within the present Barabinskaia steppe. H. Printz[3] found in the Siberian steppes remnants of a former tundra vegetation, which he attributes to the Glacial period. As Krilov proves, no evidence exists that the steppe vegetation in Western Siberia was formerly wider spread than now, i.e. Western Siberia has not had in the past a "Steppe period," analogous to that which is generally accepted for Middle and Eastern Europe. All the conclusions on the existence of such a Steppe period in Western Siberia are founded, according to him, on erroneous analogies with Europe and erroneous generalisations based on fossil animal finds[4].

The steppe vegetation of Western Siberia seems therefore to be of relatively new origin and was probably first developed in its present form in the Post-glacial epoch. On the other hand, as Penck[5] showed, steppes were widely spread in Middle and Eastern Europe at the end of the Inter-glacial and during the last glaciation (only two Glacial periods being admitted for those regions which are at a certain distance from the area of the main glaciation). It may be supposed, therefore, that when the steppe vegetation in Middle and Eastern Europe developed, the influence of the Siberian flora upon it was not especially

[1] **Andrees.** *Handatlas.* 1912, K. 139. Scale 1 : 15,000,000.

[2] **P. Krilov.** "On the Question about the Fluctuation of the Boundary between the Forest and the Steppe Provinces (Russian)." *Travaux du Musée Botanique de l'Acad. des Sciences de Pétrograd*, **14**, 82–130, 1915.

[3] **H. Printz.** *The Vegetation of the Siberian-Mongolian Frontiers*, pp. 12–13 and 40. Trondhjem, 1921.

[4] *L.c.* According to Krilov all conclusions of this kind are based on fossil finds of only two animals: the *Antilope-Sajga* (*Colus sajga*) and the Siberian marmot (*Spermophilus eversmanni*), which is quite insufficient evidence in itself alone. But the Sajga is found fossil in Western Siberia only in that area where the steppes exist to-day, and fossils of *Spermophilus eversmanni* were found only on the River Jana, in Eastern Siberia, in a locality where this animal lives still, although there are no steppes.

[5] **A. Penck.** "Die Entwicklung Europas seit der Tertiärzeit." *Rés. scient. du congrès internat. de botanique*, pp. 12–24. Vienne, 1905.

important. It is probable, indeed, that when the flora of the Siberian steppes developed, after the desiccation of the large water basins and marshes which formerly occupied the region, it received not a few of the relatively older European steppe elements. Xerophytic plants which originated in Europe and Asia mixed there together and in the course of time penetrated far into the neighbouring countries. Doubtless several Asiatic forms penetrated far into Europe. However, the extension of the direct influence, which the Siberian steppe flora had upon the European one, seems to be often overrated. It would be erroneous to draw any conclusions, by analogy, from the distribution of higher animals, whose spreading is considerably more rapid than that of plants and is not subjected to the same rules. However, even among animals, only the most rapidly moving groups show a large percentage of Siberian migrants into Europe, and not the less rapidly moving ones. Thus according to Scharff[1], the species of mammals living in Europe at the present day have, with few exceptions, migrated to our continent from other parts of the world (chiefly from Siberia). With regard to the birds it is possible that a somewhat larger number proportionally may be of European origin. Still, the great majority are to be regarded as immigrants. The autochthones are about equal to the immigrants in the reptiles, but many of the European amphibians and the majority of the fishes have probably originated on our continent. Not a single species of land or freshwater mollusc can be quoted as having migrated to Europe from Siberia in recent geological times. A very active centre of development for land mollusca lay in South-Eastern Europe, either in the Caucasus or in the Balkan Peninsula, or more probably in both. It cannot be supposed that the steppe plants were distributed in the same way as the rapidly moving higher animals, and it seems more probable that their spreading occurred in a slower way and during a longer period of time. However, even in the case of mammals, according to Scharff[2], it would be difficult to trace a limit between the Siberian and Oriental migrants, whose spreading took place across Asia Minor and may be much older than the direct migration from Siberia.

It would be no less of a mistake to consider the present centre of distribution of plant species as necessarily indicating the centre of their origin. Briquet[3] showed, and illustrated with examples, how inaccurate it would be to confound these two entirely different facts. With even greater emphasis the same may be said concerning the distribution and the origin of steppe plants, the conditions now being much less favourable for their spreading in Europe than in Asia. N. Printz[4] concluded as a result of his own investigations, that the steppes are spreading now in Western Siberia by natural means as a consequence of geological changes, which are occurring in Central Asia. This opinion finds a confirmation in the observations of Krilov and of several

[1] **R. F. Scharff.** *The History of the European Fauna*, pp. 189, 193, 196. London, 1899.
[2] *L.c.* p. 245. [3] *L.c.* p. 133. [4] *L.c.* pp. 64–67.

investigators of Central Asia, such as Huntington[1], Paulsen[2], etc. Krilov[3] proves that the steppes in Western Siberia have been constantly spreading since the Glacial period at the expense of forests and that they have never been distributed there more widely than they are now. According to these statements the steppe vegetation in Western Siberia is still advancing towards a larger development, while in Europe its maximal development was in past geological times and the present climatical conditions are less favourable to it. In such circumstances it is not impossible that even certain xerothermic species which originated in Europe are now distributed in Asia more widely than in Europe itself.

On the contrary, there are reasons for thinking that the European flora has had sources for the development of its steppe vegetation in its close neighbourhood, namely in the Mediterranean province. According to Hagen, the xerothermic element in this province is very old. There is geological evidence that at least three centres with a dry climate and a xerophytic vegetation existed in the Mediterranean as early as the Miocene times. One of them lay in the plateau of Iran; the second in N. Africa, in the district of the Moroccan Atlas; and the third in Spain, in Mezetta and the district of Ebro[4]. During the Pleistocene the climate of the Mediterranean became moister and the above mentioned xerophytic centres disappeared. There is no doubt, however, that a certain number of xerothermic species were preserved during those unfavourable times, by their growing in some limited localities under more suitable physical conditions, just as they now exist in countries with an oceanic climate. Dry and especially limestone rocks, sandy soils, and soils rich in inorganic salts might often have been places of refuge for this type of plant. Thus may be explained, with considerable probability, the often observed attachment of steppe plants to calcareous soil, which has been noted in Germany by Drude[5], in Sweden by Sterner[6], etc. Velenovsky[7] observed the same relationship in Bulgaria, and this was afterwards confirmed by other observers. Korzinsky[8], Krasnov[9], Tanfiliev[10] found the same dependence in the

[1] **E. Huntington.** *The Pulse of Asia.* Boston and New York, 1907.

[2] *L.c.* [3] *L.c.*

[4] **H.B. Hagen.** "Geographische Studien über die floristischen Beziehungen des Mediterran und Orientalischen Gebietes in Afrika, Asien und Amerika." *Mitt. d. Geogr. Ges. in München*, **9**, 144–151, 1914.

[5] **E. Drude.** *Handbuch der Pflanzengeographie*, p. 382. Stuttgart, 1820.

[6] **R. Sterner.** "The Continental Element in the Flora of South Sweden." *Geografiska Annaler*, 321–322, 1922.

[7] **J. Velenovsky.** *Flora bulgarica. Suppl.* **1**, 327, 1898.

[8] **S. Korzinsky.** "The Northern Limit of the Black-earth-Steppe Province" (Russian). *Trudy Obshtestva Estestvoispyt-pri Imp. Kazanskom Universitete*, **18**, 214–217.

[9] **A. Krasnov.** "Steppes de la Russie méridionale." *Annales de géographie*, **111**, 307–309, 1894

[10] **G. Tanfiliev.** "Die Südrussischen Steppen." *Rés. Sc. Congrès internat. de bot.* pp. 385–387. Vienne, 1905. *Phytogeographical Investigations in the Steppe Tract of Land* (Russian). St Petersburg, 1898.

South-Russian steppes themselves, and Androsovosky[1] in the steppes of Asia Minor. This phenomenon may be explained to a certain extent on the basis that the steppe plants have retained some of their older edaphic preferences.

The richly saline bottoms of dried-up sea basins, which existed in different times and in different parts of Europe, have doubtless also been places of refuge for several halophytes with xerophytic structure. Examples are well known of halophytes, inhabitants of the sea shores, growing far in the interior of the continents. Thus *Suaeda maritima, Salicornia herbacea* and other inhabitants of the European sea shores may occur as far in the interior of Asia as the Abakanskaia steppe in Siberia, etc.

The steppe vegetation probably formed gradually and changed its composition in the course of time, corresponding to the changes of the climate and the salt content of the soil. In its earlier stages the soil of present South Russia and Hungary, being bottoms of former seas, was certainly rich in inorganic salts. It seems, however, that no direct connection existed at that time between Europe and Central Asia, because the characteristic representatives of the saline steppes and deserts of Turkestan are almost completely lacking in the Hungarian and the largest part of the South Russian steppes.

During all the stages of the development of the European steppe flora a direct immigration from the Mediterranean and its neighbouring countries may be more easily imagined than the often supposed migration in large numbers from the foot of the Altai, along a kind of relatively narrow corridor in Western Siberia. We have no ground for believing that the Altai itself had an especially great importance as a centre of development for the steppe vegetation. According to Krasnov[2] geological and phytopalaeontological data witness that a wet climate existed there during the Tertiary. It is possible that a certain number of steppe plants developed afterwards on dry rocks of the southern slopes and closed valleys of Altai, as Krasnov supposes. It can, however, be hardly supposed that the plants thus originating were of greater importance for the steppe vegetation of Europe than those originating in the same way during the dry period in the mountains of Europe itself and in its neighbourhood, such as the South Urals, Caucasus, the mountains of the Balkan Peninsula, of Middle Europe, etc. Doubtless many xerophytes originated in the interior of Asia and penetrated into Europe through the Uralo-Caspian gate. However, among all the ways which lead from the interior of Asia to Europe, this one could be used only for the relatively shortest time, which reduces its importance. Typical representatives of the Turkestan flora could spread in large numbers only as far as the Volga[3].

[1] **T. Androsovosky.** "Vorläufiger Bericht über die im Jahre 1911 in den Steppen Kleinasiens ausgeführte Reise." *Botanikay Kozlemenyek*, **11**, 16–21, Suppl., 1912.

[2] **A. Krasnov.** "Notices sur la végétation de l'Altai." *Scripta botan. Norti Univ. Petrop.* **1**, 183–214, 1886.

[3] **A. Beketoff.** "Sur la flore du gouvernement de Yekaterinoslav." *Scripta botan.* **1**, 32, 1886.

Xerothermic plants doubtlessly existed in many localities around the Mediterranean and especially in the neighbourhood of the old xerophytic centres, i.e. of Iran and the Iberian peninsula. From there they could easily find their way to the European steppes. These ways of distribution may be traced in several cases. Thus according to Briquet, the xerothermic plant element in the Western Alps came from Piedmont[1]. From the works of Beck[2] and Hayek[3] the influence which the flora of the Karst exercised upon the Pannonian steppe vegetation is known.

Many xerothermic plants undoubtedly immigrated into South-East Europe from Iran and Asia Minor either along the western shores of the Caspian Sea or along the western shores of the Black Sea. The researches of Medwedew, and especially his very instructive map of the Caucasus[4], show us the route of the migration through that country. The steppe vegetation in Eastern Cis-Caucasia is directly related, according to him, to the vegetation of the dry districts of Transcaucasia. This vegetation spreads far into the interior of Transcaucasia along the valleys of Kura and Arax; it reaches the foot of Ararat and Erivan in the Armenian plateau. This vegetation is also closely related to the steppe formations of Asia Minor and Armenia[5]. On the contrary, the steppe vegetation of Western Cis-Caucasia does not show the same close relationship to Transcaucasia and Iran. These facts are easily understood, because between the two districts lies a barrier, in the shape of the moist and forested South-Euxinian zone (in the sense of Engler), which occupies the western part of Transcaucasia and the north-eastern shore of Asia Minor and which represents remnants of a thermophilous Tertiary vegetation.

No similar barrier exists west of the Black Sea, i.e. in the eastern part of the Balkan Peninsula. There are neither high mountains nor large spaces with moist climate, only a small one in the district of Strandja, which is the last outpost of the South-Euxinian vegetation. Besides this, the communication between Europe and Asia through the Balkan Peninsula is older than that across the Caucasus. In past geological times a broad connection existed between the Balkan Peninsula and Asia Minor, across the Archipelago, whereby a mass migration of plants was possible. According to C. and E. Reid[6], whose opinion is based on phytopalaeontological data, a large number of species among the present temperate vegetation of Europe immigrated by this way from Asia

[1] *L.c.* pp. 172–173.

[2] **G. Beck von Mannagetta.** "Über die Bedeutung der Karstflora in der Entwicklung der Flora der Ostalpen." *Rés. scient. congrès bot.* pp. 174–178. Vienne, 1905.

[3] **A. Hayek.** "Pontische und pannonische Flora." *Oesterr. bot. Zeitschr.* pp. 231–235, 1923.

[4] **J. Medwedew.** "Über die pflanzengeographischen Gebiete des Caucasus." *Moniteur du Jardin Botanique de Tiflis*, Livr. **8**, 1–66, 1907.

[5] *L.c.* p. 46.

[6] **C.** and **E. Reid.** *The Pliocene Flora of the Dutch-Prussian Borders*, pp. 22–23. The Hague, 1915. **E. Reid.** "Recherches sur quelques graines pliocènes du Pont-de-Gail." *Bull. Soc. Géol. de France*, **20**, 52–57, 1920.

during the second half of the Tertiary. Xerothermic plants could also reach Europe through this immigration. There is geological evidence that centres with dry climate existed during a part of the Tertiary both in Iran and also in Central Asia[1]. The existence of an extremely large number of endemics in the xerophytic vegetation of Turkestan, with many endemic genera and several monotypes among them, speaks in favour of this opinion[2].

Zoogeographical data also affirm the existence in the past of a large Oriental immigration into Europe. It is characteristic that this immigration is especially well expressed in those groups of animals which are biologically attached to definite plant species, and can therefore migrate only together with them. Such is the case of butterflies. A large number among them are supposed to have originated in South-West Asia, as for example the genera *Papilio*, *Thais*, *Parnassius*, *Colius*, *Danaja*, etc.

In all cases, when the vegetation of a certain country has not been previously completely destroyed by some phenomenon, like extensive glaciation, it is always most probable to suppose that the migration of plants between that country and a neighbouring one occurred in both directions, that is to say consisted in an exchange of plants between the two countries. Such an exchange probably took place between Europe and Asia in Pre-glacial times Thus in the flora of Turkestan, genera are represented whose chief distribution and apparent place of origin lie in the Mediterranean province. In this way the vegetation of the Mediterranean and that of the Asiatic Steppe province mixed together so closely, that now they can hardly be distinguished from each other by phytogeographers. Thus may also be explained why many xerothermic plants could afterwards spread, in a relatively short time, through the steppes of Europe and Siberia and be represented in both by parallel forms (as, for example, the sect. *Pulsatilla* of the genus *Anemone*[3]). The Oriental immigration doubtless had a great influence upon the xerothermic vegetation of Bulgaria. Among 226 Bulgarian plants, which Velenovsky[4] listed as having originated in Asia Minor and Armenia, a large number are xerothermic species. The route of the Oriental immigrants may be clearly observed in the vegetation of Bulgaria and the neighbouring countries. Some of them have only reached as far as the European shore of the Marmara sea, Bosphorus or Dardanelles, as for example *Silene chloraefolia*, *Dianthus lydus*, *Astragalus anatolicus*, *A. trojanus*, *Gonocytisus angulatus*, *Hedysarum varium*, *Onobrychis cana*: others reached the foot of the Rhodope,

[1] **J.** and **C. Gregory.** "The Geology and Physical Geography of Chinese Tibet." *Philos. Trans. of the Royal Soc. of London*, pp. 257–258, 1925.

[2] **B. Fedchenko.** *The Vegetation of Turkestan* (Russian). Petrograd, 1915. More than 35 endemic genera, among which more than 20 are monotypic. About 50 genera have distributional areas both in Turkestan and the East Mediterranean (in the sense of Engler).

[3] Numerous closely related species are widely spread in Europe, the Orient and Asia. Cf. **A. Hayek.** "Kritische Übersicht über die Anemone-Arten der Section *Campanularia* Endl." *Festschr. zur Feier des siebz. Geburtstages P. Ascherson*, pp. 451–475. Leipzig, 1904.

[4] *L.c.* pp. 311–314.

thus *Aristolochia hirta, Rhazia orientalis, Genista anatolica.* Several species stopped in their migration towards the north at the foot of the Balkan range, thus *Aethionema buxbaumii, Cleome aurea, Polygala rhodopea, Centaurea monacantha,* the spinescent representatives of the genus *Astragalus,* sect. *Tragacantha,* etc. Many other species doubtless spread farther north along this route and reached South Russia. Thus of the abundant Oriental species of the genus *Celsia* four reached Bulgaria, but only one of them penetrated as far as South Russia. The genus *Verbascum,* after its immigration into the Balkans, received here a new development and is represented now in the Bulgarian flora by more than 30 species, mostly xerothermic plants. Of the eight species of *Verbascum,* which Krasnov records for the South-Russian steppes, six are found also in Bulgaria and the other two grow in the Caucasus and Armenia.

The above mentioned *Jurinea tzar-ferdinandi,* which occurs in Bulgaria and has the character of a relict plant, connects the South-Russian *Jurinea stoechadifolia,* belonging to the Sect. *Linearifoliae,* with the representatives of the Asiatic Sect. *Stoechmanniae.* Many more such examples could be quoted.

Corresponding to the geographical situation of Bulgaria, which lies at the boundary of the Mediterranean province, the influence of the Mediterranean flora is especially strong among xerothermic plants. A very large number among these plants belong to the Mediterranean vegetation. On the contrary, species which may be supposed to have immigrated into Bulgaria direct from Siberia, through the Uralo-Caspian gate and South Russia, are very few, even among plants commonly regarded as forming a steppe element. From this point of view interesting results may be obtained by examining a list of Bulgarian "steppe plants." Considering that the conception of "steppe plants" is not a very definite one and in order to avoid making an arbitrary choice, we shall examine only that group of Bulgarian plants, which Krasnov listed, among others, as characteristic representatives of the South-Russian steppe vegetation. Firstly it must be noted that the above mentioned species grow in Bulgaria under very various ecological conditions. Thus we meet among them several inhabitants of meadows such as *Thalictrum minus, Clematis integrifolia, Trifolium montanum, Polygala vulgaris, Orobus albus,* or even of swampy meadows, such as *Leucojum aestivum.* Others among them are representatives of the forest vegetation, as for example *Myosotis silvatica.* Many of them grow on rocks, thus *Dictamnus fraxinella, Silene longiflora, Cotoneaster vulgaris, Convolvulus cantabricus,* etc. Several are ruderal or half-ruderal plants, as for example *Eryngium campestre, Tordylium maximum, Inula salicina, I. hirta.* Chiefly on sand and rocks of the sea shore may be found *Helichrysum arenarium, Artemisia maritima, Ephedra vulgaris.* Also predominantly in the warmest parts of the country grow *Ceratocephalus orthoceras, Linum flavum, L. hirsutum, L. tenuiflorum, Haplophyllum suaveolens,*

Salvia aethiopis, etc. Others among them are on the contrary representatives of the subalpine belt of vegetation in high mountains, thus *Libanotis montana*, *Antennaria dioica*, *Sanguisorba officinalis*. Especially on subalpine and alpine rocks grows *Scutellaria alpina* (1700–2500 metres above the sea). The ecological history of the steppe vegetation has perchance left its traces in this various distribution of steppe elements.

Another interesting result may be obtained if we divide these plants both according to their geographical distribution and systematic relationship. In this way an approximate conclusion concerning their origin may be reached. Thus firstly we find a group of species which may be supposed to have grown in Europe even in Pre-glacial times. Such is a group of plants which have a circumpolar distribution or a very large distributional area in the warm belt:

Ranunculus acer	Myosotis silvatica	Festuca ovina
Turritis glabra	Euphrasia officinalis	Koeleria cristata
Antennaria dioica	Plantago media	Tragus racemosus*
Achillea millefolium	Andropogon ischaemum*	Hierochloe odorata

* Widely spread through the warm temperate and tropical zones of both hemispheres.

In the Pre-glacial strata in Europe were found:

Sanguisorba officinalis	Cotoneaster vulgaris	Thymus serpyllum

An old origin or an old immigration into Europe may be supposed also for a group of plants which have a large area both in Europe and Asia and also systematically related forms in both continents and often also in America. To this group belong: *Thalictrum minus* (a large distributional area; found in the lower Glacial strata in Europe), *Anemone silvestris* (a large distributional area; and related forms both in Europe and Asia), *Dictamnus fraxinella* (a monotypic genus with a very large distributional area), *Vicia tenuifolia* (a large distributional area and relations in Europe and Asia); *Filipendula hexapetala* (a large distributional area; the only closely related species, *F. ulmaria*, is found in Pre-glacial strata in Europe); *Fragaria collina*, *Bupleurum falcatum* (a large distributional area; related forms in Europe, Asia and South Africa); *Turgenia latifolia* (a monotypic subgenus, widely spread in Europe and Asia through the Orient); *Antirrhinum orontium* (a monotypic section, covering a large area in Europe, Asia and N. Africa); *Ajuga genevensis* (a large distributional area; related forms both in Europe and Asia; the closely related *A. reptans* is found in Pre-glacial strata in Europe), *Ephedra vulgaris*, *Pulsatilla vulgaris*, *P. patens*, *P. pratensis*.

Especially large is the number of species, which have both their distributional area and chief relatives in the Mediterranean province (in the large sense) or in its close neighbourhood. As such may be listed:

Ranunculus illyricus	Helianthemum oelandicum	D. trifasciculatus
Erysimum odoratum	Polygala major	D. atrorubens
E. cuspidatum	P. vulgaris	D. carthusianorum
Alyssum argenteum	P. comosa	D. campestris
A. calycinum	Dianthus armeria	Gypsophila glomerata
A. tortuosum	D. pseudarmeria	Silene compacta
Camelina microcarpa	D. capitatus	S. longiflora

Alsine tenuifolia
Linum flavum
L. tauricum
L. nervosum
L. austriacum
L. hirsutum
L. tenuifolium
Haplophyllum suaveolens
Rhus cotinus
Genista tinctoria
Cytisus capitatus
C. austriacus
Anthyllis vulneraria
Glycyrrhiza echinata
Astragalus ponticus
A. dasyanthus
Coronilla varia
Onobrychis gracilis
Orobus albus
O. canescens
Dorycnium herbaceum
Potentilla opaca
P. patula
Herniaria hirsuta
H. incana
Bupleurum rotundifolium
Pimpinella tragium
Seseli tortuosum
Tordylium maximum
Peucedanum ruthenicum
Asperula cynanchica
A. tinctoria
A. glauca
A. tyraica
Galium mollugo
Valeriana tuberosa
Cephalaria transsilvanica
Inula ensifolia
I. squarrosa
Echinops sphaerocephalus
E. ritro
E. exaltatus
Xeranthemum annuum
Centaurea solstitialis
C. marschalliana
C. scabiosa
C. montana
C. orientalis
C. salonitana
C. ovina*
C. diffusa
Scorzonera mollis
Taraxacum serotinum
Lagoseris orientalis
Phyteuma canescens
Campanula bononiensis
Vinca herbacea
Vincetoxicum officinale
Anchusa barrelieri
A. stylosa
Nonnea pulla
Echium rubrum
Onosma echioides
Convolvulus cantabricus
Verbascum speciosum
V. phlomoides
Verbascum lychnitis
V. phoeniceum
V. blattaria
Veronica austriaca
Odontites rubra
Pedicularis comosa
P. campestris
Salvia aethiopis
S. austriaca
S. nutans
S. pendula
S. verticillata
Teucrium polium
Stachys recta
S. angustifolia
Ajuga laxmannii
Euphorbia nicaensis
E. agraria
Crocus biflorus
C. speciosus
Aegylops cylindrica
Andropogon gryllus
Anthericum liliago
A. ramosum
Allium moschatum
A. flavum
Muscari racemosum
M. botryoides
Hyacinthus leucophaeus
Ornithogalum nutans
O. umbellatum
O. fimbriatum
O. tenuifolium

* In Bulgaria represented by a form.

The following species are distributed both throughout the Mediterranean Region and also far into the interior of Asia. Their chief relations are, however, in the Mediterranean province, wherefore their origin is most probably a Mediterranean one:

Ceratocephalus orthoceras
Ranunculus oxyspermus
Sisymbrium strictissimum
Erysimum repandum
Alyssum campestre
Isatis tinctoria
Helianthemum vulgare
Tunica prolifera
Silene conica
S. viscosa
S. supina
Hypericum elegans
Lavatera thuringiaca
Linum perenne
Medicago falcata
Trifolium montanum
T. alpestre
Astragalus cicer
A. onobrychis
A. exscapus
A. vesicarius
A. albicaulis
Lathyrus tuberosus
Sanguisorba minor
Eryngium campestre
Falcaria rivini
Trinia kitaibelii
Galium verum
Knautia arvensis
Scabiosa ochroleuca
Aster amellus
Inula salicina[1]
I. hirta[1]
I. oculus christi[1]
Helichrysum arenarium
Achillea setacea
Pyrethrum corymbosum
P. millefoliatum
Artemisia maritima
A. pontica
A. austriaca
Senecio jacobea
S. erucifolia
S. doria
Jurinea arachnoidea
Tragopogon major
T. orientalis
T. brevirostris
Campanula sibirica (Caucasian or Iranian origin)
C. rapunculus
Statice tatarica
S. latifolia
Echinospermum patulum
Rindera umbellata
Verbascum nigrum
Linaria genistaefolia
Veronica teucrium[2]
V. spicata[2]
V. spuria[2]
Origanum vulgare
Salvia silvestris
Nepeta pannonica
N. ucranica
Scutellaria alpina
Teucrium chamaedrys
Sideritis montana
Euphorbia gerardiana
Poa bulbosa
Iris pumila
Asparagus officinalis
Allium verticillatum
Ornithogalum narbonense
Gagea pusilla
Thesium ramosum

[1] Cf. **G. Beck.** "Inulae europeae." *Denkschr. Akad. Wiss. Wien*, **44**, 1881.
[2] According to **E. Wulf.** *Crimo-Caucasian species of the Genus Veronica* (Russian), 1915.

Another group of species is widely spread through the Mediterranean (the Orient) and the interior of Asia; their relations lie in Asia or are vague. This group represents most probably the Oriental immigration. To this group belong:

Adonis vernalis*	Artemisia campestris	Stipa capillata
Erysimum canescens	A. scoparia	S. pennata
Gypsophila paniculata	Chondrilla juncea	Triticum cristatum
Glycyrrhiza glabra	Androsace maxima	Linosyris vulgaris
Astragalus austriacus	A. elongata	L. villosa
Spiraea crenifolia	Phlomis tuberosa	Kochia prostrata
Libanotis montana	Euphorbia virgata	

* The immigration route is not completely clear; it may have been the Siberian one, but more probably was across the Caucasus.

Some of them may have immigrated into Europe through the Caucasus. *Kochia prostrata* may as likely be of European as of Asiatic origin; its spreading, however, occurred probably through the Orient.

The following species have their distributional area and relationship chiefly in Europe, yet not in its Mediterranean part: *Ranunculus polyanthemos*, *Hesperis tristis* (Pontic distribution and relations), *Viola hirta*, *Arenaria rigida* (Pontic distribution, relations in the Mediterranean province and in Asia), *Geranium columbinum*, *Potentilla recta* (Pontic origin, according to T. Wolf[1]), *P. inclinata*, *P. argentea*, *Peucedanum alsaticum*, *Serratula heterophylla*, *S. tinctoria*.

The following species are spread through Eastern Europe and Siberia, but are lacking in the Orient; their distribution may be supposed to be the result of a direct exchange between Europe and Siberia through the Uralo-Caspian gate: *Paeonia tenuifolia* (the origin is not quite clear, it may be South Uralian, North Caucasian or West Siberian); *Silene chlorantha* (most probably of European origin but spread far towards the east); *Caragana frutescens* and *Astragalus testiculatus* are of Asiatic origin and their immigration into Europe occurred probably directly from Siberia, although possibly through the Caucasus. *Amygdalus nana*, *Prunus chamaecerasus* and *Adenophora liliifolia* may be considered as direct immigrants from Siberia.

Thus among the named steppe element in Bulgaria the number of species which may be supposed to be direct immigrants from Siberia is very insignificant, especially in comparison with the number of species which have probably originated in the Mediterranean province (in a broad sense). It must be emphasized, however, that the above analysis and its results cannot claim to have an absolute value. Neither the geographical distribution nor the present taxonomic relationship by itself is able to show with certainty the place of origin of a species. The inexactness of both methods of investigation has been proved by Kerner[2] and Briquet. By neither method can more than a certain probability be reached. Therefore on the basis of the above analysis

[1] "Monogr. d. Gatt. *Potentilla*." *Bibliotheca Botanica*, N. F. **1**, 1908.

[2] *Pflanzenleben*, II. 838, 1891.

only one general conclusion can certainly be reached, that the so-called "steppe plants" in Bulgaria are chiefly of Mediterranean origin.

Considering the geographical situation of Bulgaria this result is very natural, especially if we remember that even in the South-Russian steppes of the government Yekaterinoslav, Beketoff found a larger number of Oriental (Caucasian) immigrants than of plants which had migrated direct from Turkestan and Siberia[1].

From the circumstance that among plants common to Bulgaria and the South-Russian steppes the Mediterranean elements prevail, it is evident that the migration of plants between the two countries occurred chiefly in the direction from south towards north, and to much less extent in the opposite direction. This migration occurred probably as the climate was gradually becoming warmer after Glacial times and as a result of the climatic changes.

[1] *L.c.* pp. 75–78.

SOIL SOURNESS AND SOIL ACIDITY

By W. H. PEARSALL.

(*With one Figure in the Text.*)

In a recent number of this Journal (**14**) criticisms have been directed at a suggestion put forward by the writer in 1922 to explain some cases of soil sourness (**11**). Since these criticisms appear to be founded upon a misconception and mis-statement of the original suggestion it is necessary to refer to them in some detail and the opportunity may also serve to draw attention to some of the problems facing the student of the subject.

The majority of investigators fail to distinguish *soil sourness* from *soil acidity* (or the hydrogen ion concentration of the soil). These two factors are usually associated in nature but they are not of necessity the same nor even interdependent. There are, of course, a number of factors which also are often or usually found in soils which are sour, e.g. deficient nitrification, deficient aeration, high organic content, organic soil toxins. It is advisable to keep all of these factors in mind in discussing the phenomenon of soil sourness for any of them may serve to prevent the growth of normal plants on sour soil. The heathy plants which are found on sour soils in nature are clearly able to withstand all the factors which normally occur in such soils and it appears to be true that these plants are also "calcifuge" and unable to grow on normal soils. The problem thus assumes great complexity. We have not only (i) to determine the factors which prevent normal plants from growing on sour soils but we have also (ii) to find an answer to the question why heathy species *can* grow on sour soils, but (iii) cannot grow on normal soils. These three groups of problems *may* be different aspects of the same problem. The present evidence, however, suggests that they are not.

Turning now to the soil side of the problem, we have first to recognise that soils may apparently be *sour* and yet only slightly or not at all *acid*. This is another aspect of the fact, to be considered in detail below, that the distribution curves of species in relation to the hydrogen ion concentration, overlap enormously. We may thus find heathy species growing profusely on soils whose pH value lies between 6 and 7. In order to explain cases of this kind the writer suggested in 1922 that soil sourness might be attributed (*a*) to calcium deficiency in the soil and (*b*) to a high proportion of potassium and sodium to calcium (and magnesium). This suggestion was based on the examination of the waters of some nearly neutral gravels on which *Calluna* and *Nardus* were growing, together with the known fact that calcium leaches

from normal colloidal soils more rapidly than potassium and sodium. Leaching is one of the principal causes of soil sourness and it clearly leads to an increase in the $\frac{K + Na}{Ca}$ ratio in the soil (**11**). The problem is capable of being attacked from another angle. If heathy plants can only grow on soils deficient in calcium then the basic ratio *must* be of fundamental importance to them, because the physiological effects of calcium can be "antagonised" or removed by potassium and sodium. The literature is full of instances of this fact and we may be pardoned for not taking specific cases in detail. The position of magnesium in regard to these physiological activities is intermediate. It "antagonises" both potassium and sodium, and also calcium. Since, however, the principal factor in determining the basic ratio in soils is calcium deficiency, the behaviour of magnesium is, at the moment, of small importance except in those soils where it is present in predominant quantities.

Dr Salisbury (**14**) has recently subjected the suggestion outlined above to some detailed criticism, although the value of his criticisms is considerably lessened by the fact that he has not even stated the basic ratio hypothesis correctly, for he describes it as the "ratio between *calcium and sodium* and *potassium and magnesium*." (The italics are his.)

His criticisms are (1) that the chemical composition of the soil solution cannot be inferred from soil analyses, and that the proportions of potassium extractable from soils are subject to great variations in relation to the water content of the soil; (2) that the basic ratio hypothesis involves the assumption that plants of calcareous soils are intolerant of high potassium contents and that the Rothamsted manurial experiments indicate that soil acidity is lessened by the addition of potassium salts; (3) that Masall's results indicate that the growth of wheat in water cultures is related to hydrogen ion concentration rather than to the basic ratio.

The impartial critic would doubtless agree that all of these arguments are irrelevant so far as the published statements of the basic ratio hypothesis are concerned. Nevertheless we will consider these points in detail.

1. If the composition of the soil solution cannot be inferred from soil analyses, then we cannot use such data to argue for or against the hypothesis under consideration. This hypothesis was not, however, based primarily on soil analyses, but (*a*) on analyses of water washed through gravel or flowing through it; (*b*) on the known facts of leaching and base exchange in normal soils. Further, one cannot imply, as does Dr Salisbury, because it is difficult to obtain information about the soil solution, that the composition of this solution has little or no effect upon the plants growing in it.

The only grounds on which we can infer the possible composition of the soil solution, namely, from the expressed soil waters, from drainage waters, water extracts, acid extracts, and salt extracts, all alike indicate that the calcium content of the soil is subject to great variation in different soils and

is lowest in sour and acid soils. In regard to the basic ratio, our information is limited since analysts do not usually estimate all the soil bases. By the salt extraction method, Kelley and Brown (**8**) have shown that the replaceable bases of acid soils possess a basic ratio averaging about twice that of normal soils, although their results exclude the calcium carbonate present, and hence give a much higher basic ratio for the normal soils than would really exist. Olsen's figures (**9**), which are summarised below, refer to extracts with water saturated with carbon dioxide, but they similarly indicate a higher basic ratio for acid soils.

	No. of soil					
	6	14	7	18	20	19
*p*H value	4·9	4·9	6·1	6·2	6·2	7·3
$\frac{K + Na}{Ca + Mg}$	0·95	1·13	0·25	0·20	0·14	0·16
$\frac{K + Na}{Ca}$	1·32	1·30	0·27	0·21	0·14	0·19

Olsen (**9**, **10**) also supplies larger numbers of partial analyses giving only the potassium and calcium contents of the carbonated water extracts. These also show that a higher K/Ca ratio occurs in such extracts from acid soils, and there is a certain amount of variation in the ratio for slightly acid soils, so that we have clearly to keep acidity and the basic ratio distinct as soil factors. They are not exactly proportional.

Dr Salisbury's criticism that the amount of potassium extractable from soils is subject to great variation in relation to the soil water content, does not appear to me to be of much value. Some of the most important soil properties may be subject to great variation, as, for example, its water content and nitrate content. But Dr Salisbury makes the astonishing statement that these fluctuations are shown in "determinations based on the actual soil solution." This statement is incorrect, since the fluctuations are obtained by comparing the expressed soil solutions, from soils containing *at most* 23 per cent. of water, with the water extracts (one part soil to five water) which represent a "water content" of 500 per cent. (Burgess, **3**). It is not justifiable on these data alone to infer that the potassium content of the soil solution from any single soil is subject to great variations under natural conditions, especially since in the figures given by Burgess there is no relation between the amount of soil moisture and the potassium content of the soil solution for the different soils examined. The whole argument, however, is irrelevant. If we are to consider the basic ratio hypothesis, then we require to compare the calcium content of the soil solution and its basic ratio. The data given by Burgess (**3**) indicate, as far as their completeness and analytical precision will allow, that the two factors we require fluctuate in the same directions in the water extract as they do in the soil solution. The soils with the highest basic ratios in the water extracts are those with the highest basic ratios in the expressed solutions.

2. The basic ratio hypothesis does not necessarily involve the assumption that the plants of calcareous soils are intolerant of high proportions of potassium. It does not refer to such soils or to such plants (**11**) and it was, in fact, expressly stated in such a form as to refer only to soils poor in calcium. There are obvious reasons for this. At least two classes of soils exist which may be relatively rich in calcium salts and which have also a high basic ratio, namely, (1) salt marsh and similar marine soils, (2) "alkali" soils as found in arid regions. While the plants of these habitats may have some similar structural features to those of sour soils, we have at present no other justification for comparing them. The further criticism that the addition of potassic manures to the Rothamsted plots has not increased the acidity or sourness of these plots, is thus beside the point, since the soils used are relatively rich in calcium. Further, the addition of potassium salts to soil does not necessarily increase either the content or proportion of potassium in the soil solution. The actual result of such a treatment will vary with the nature of the treated soil. In the case of a calcium rich normal soil like that at Rothamsted, the probable result of adding potassium salts would be that the potassium would be "adsorbed" by the soil, while other bases, and *principally calcium*, would replace it in the soil solution. That some such change takes place at Rothamsted may be inferred, not only from the increase in the production of leguminous species, but also from Voelcker's analyses of the drainage waters, which show little or no change in the potassium content but a very largely increased proportion of calcium (**6**). It cannot be argued that this would always be the result, for if the soil were deficient in bases, iron and aluminium would be liberated on adding the potassium salt, as in Comber's test for soil sourness (**5**). There may also be a third case, that of acid peaty soils deficient in iron and aluminium, where the addition of neutral potassium or calcium salts may cause a decided increase in hydrogen ion concentration. The origin of this increased acidity is at present unknown.

It is necessary to enlarge on these points in order to demonstrate that one must be very cautious in arguing from manurial experiments, unless fairly precise data as to effect are available. The considerations outlined above, however, suggest a possible cause for the well-known fact that soil sourness is removed most thoroughly by lime and not by addition of any calcium salt. Remembering that soil sourness and soil acidity are usually associated, then we have probably two extreme cases to consider:

(1) The addition of lime removes both sourness and acidity.

(2) The addition of calcium salts of strong acids, e.g. chlorides, sulphates, removes calcium deficiency but *increases* acidity.

In the second of these cases, a high hydrogen concentration may still remain as a bar to the growth of normal plants, so that this treatment would not materially improve the crop-producing power of the soil.

3. Dr Salisbury accepts and refers to Masall's results that wheat shows a definite optimum growth in relation to hydrogen ion concentration but none in relation to the basic ratio of the culture medium. It may be pointed out that the basic ratio hypothesis was not devised to account for the growth of wheat, but as an explanation of the distribution of heathy plants. The fact that different species behave in very different ways is beautifully illustrated by the case of barley. This cereal is extremely sensitive to soil sourness (much more so than wheat) but less sensitive to high hydrogen ion concentrations (Olsen, **10**, Arrhenius, **2**). There are grounds for believing that high proportions of available aluminium may be the toxic element in sour soils in this instance (Olsen, **10**, Hartwell and Pember, **7**) and an analogous case is apparently that of the tea-plant (**4**).

On the other hand, Olsen (**10**) found that barley alone of the acid and alkaline soil plants he tried was sensitive to aluminium. It is, therefore, pretty clear that we cannot apply either the barley or the wheat result to other plants without further evidence. A variety of reasons have been suggested (and on good evidence) to account for the inability of normal plants to grow on sour and acid soils and individual species may well be limited to normal soils by their inability to grow well in the presence of any one of the following factors, viz. (i) high hydrogen ion concentration, (ii) low calcium content, (iii) low calcium and high proportion of aluminium and/or iron, (iv) low calcium and high basic ratio, (v) organic toxins, (vi) scarcity of available nitrogen, (vii) scarcity of oxygen. It would be folly to assert, in the present state of our knowledge, that any one of these factors kept off all normal species from sour soils. Advocates of the case for hydrogen ion concentration (Olsen, **10**, Salisbury, **14**) overlook two very important points: (i) that sour soils exist which are not or only slightly acid, (ii) that the limits of distribution in nature, and even of successful growth, occur at very similar hydrogen ion concentrations for perhaps the majority of species. For example, the distribution curves for *Pteridium aquilinum* and *Vaccinium myrtillus* (or for *Ficaria* and *Mercurialis*) given by Salisbury (**14**) show remarkable similarity and it is clearly not permissible to assume that hydrogen ion concentration exerts any appreciable rôle in differentiating their distribution in the localities examined, although possibly most ecologists would regard *Vaccinium* as the plant more characteristic of sour soils. Even when the average distribution curves show different modes, e.g. *Vaccinium myrtillus* and *Mercurialis perennis*, there is often a very considerable overlap of the pH ranges, and this may be much greater for the species mentioned than is indicated by either Olsen (**10**) or Salisbury (**14**). For instance, in the Crag Woods (N. Lancs.) *Mercurialis* grows in abundance between pH 4·9 and 6·2, while the similar values for *Vaccinium* in these woods were pH 4·2 to 6·0. We are not justified in saying that hydrogen ion concentration determines the distribution of these species in this instance. On the other hand, all the *Vaccinium* soils tested

were "sour" with Comber's thiocyanate test (**5**), while those under *Mercurialis* were not. It is, in this instance, reasonable to attribute soil sourness to the quantity and character of the soil bases, and this, rather than the *p*H value, appears to be associated with the distribution of the vegetation.

A similar overlapping of ranges of hydrogen ion concentration, which is of interest, is that shown by *Phragmites communis* compared with *Eriophorum* (either *vaginatum* or *angustifolium*). The *p*H ranges (not necessarily extreme for these plants) are *p*H 7·7–5·0 (*Phragmites*), 7·0–3·7 (*E. angustifolium*) and 6·1–3·5 (*E. vaginatum*) for localities where the species were abundant but not intermixed. These results are of interest because both *Phragmites* and *Eriophorum* are tolerant of high proportions of aluminium (Stoklasa, **16**) and we seem to have here a case in which neither aluminium nor acidity can be regarded as the decisive factor over the overlapping ranges.

These instances are only a few among the many which might be cited. We can state the problem in a more general, yet equally definite way. Practically all species are able to grow abundantly on soils whose *p*H value lies between *p*H 5 and 6·5, yet some of these soils bear "sour" types of vegetation and others do not.

One other point remains to be considered. What importance are we to attach to curves showing the incidence of species in relation to the hydrogen ion concentration of the soil? Salisbury (**14**) appears to attach considerable importance to these curves in spite of the objections to which they are open, and his results may be taken as representative. In actual fact such curves require very careful analysis before any arguments can be based on them. The need for analysis will be apparent from the following considerations. Curves showing the incidence of a species in relation to any variable soil factor would presumably obey the general rule and show a "mode" comparable to the "mode" shown in Salisbury's curves. We require, at the very least, to know if the differences between the various modes (for different species) are significant or not. From the overlapping nature of the curves this appears to be improbable. Furthermore, no attempt is made to eliminate the influence of the curve, showing the relation of number of soils examined to the various *p*H classes. Olsen (**10**) has attempted this by expressing his results as "percentage frequencies" or as "percentages of localities examined." Presumably Salisbury's curve for *Psamma* "frequency" at Blakeney Point is of the same sort, though information on this vital point is lacking. Even so it cannot be claimed that the influence of the "soil curve" is eliminated. According to Salisbury's own data (**15**) about 62 per cent. of the Blakeney beach and dune soils lie between *p*H 6·9 and 7·2, and it is therefore extremely probable that *Psamma* will be most frequent at these *p*H values (see Fig. 1).

Salisbury further draws attention to what he characterises as the "bimodal" incidence curve shown best by *Fagus*, *Mercurialis* and *Ficaria*. All of these species show modes at the same places, *p*H 6–6·5, and *p*H 7–7·5. Now

Salisbury gives no data as to the number of soils examined in each of the pH classes, so that the influence of the "soil curve" on these modes cannot be estimated. My own random collection of soil pH values (for north of England woodlands) includes a fair range of both siliceous and calcareous soils and will, perhaps, serve to indicate the effect of the number of soils occurring in each of the pH classes. Curiously enough, the data show modes at precisely the

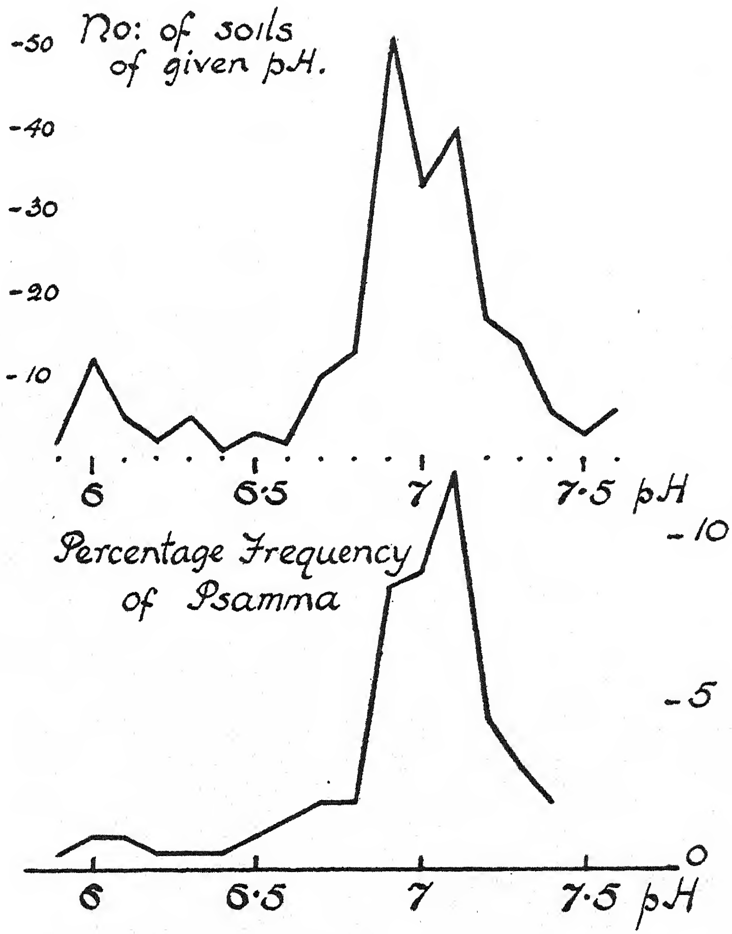

FIG. 1. The curves for "Percentage Frequency" of *Psamma* at Blakeney and the number of soils recorded by Salisbury at each pH value for the beaches and dunes at Blakeney Point.

*p*H values at which the modes for the incidence curves occur in the cases mentioned above:

*Numbers of recorded p*H *values for soils of different types.*

	*p*H class							
	4–4·4	4·5–4·9	5–5·4	5·5–5·9	6–6·4	6·5–6·9	7–7·4	7·5–8
1. Calcareous (Yorks.) ...	—	—	—	—	8	19	31	12
2. Calcareous clay (N. Lancs.)	—	2	4	9	17	14	26	4
3. Siliceous*	10	41	26	29	30	11	3	—
Total ...	10	43	30	38	**55**	44	**60**	16

* Carboniferous and Red Sandstones, Silurian.

The bimodal incidence curve, for the three species under discussion, is clearly suspect, especially since all of these three species occur both on calcareous and siliceous soils. Still further examination reveals other objections to the bimodal incidence curve. It is not shown in Olsen's data for either *Mercurialis* or *Ficaria* (**10**), and for the relatively few cases in which he obtains a bimodal curve (*Festuca* and *Taraxacum*) Olsen puts forward the suggestion that the species includes different sub-species which tend to occur at different hydrogen ion concentrations. Secondly, data from the north of England for the distribution of *Mercurialis* in relation to hydrogen ion concentration do not indicate a bimodal form. In fact the maximum number or percentage of occurrences occurs in the region (*p*H 6·5–6·9) given by Salisbury as the depression between two modes.

*p*H *values of soils on which* Mercurialis *was abundant.*

	*p*H class						
	4·5–4·9	5–5·4	5·5–5·9	6–6·4	6·5–6·9	7–7·4	7·5–8
No. of records...	1	5	6	8	**16**	9	2
% of total soils*	2·3	16·6	15·8	14·5	**36·3**	15·0	6·2

* Percentage of the total number of woodland soils examined in each *p*H class.

Thus the bimodal incidence curve cannot be regarded as a satisfactory basis for argument, until the data have received careful statistical analysis and until the present discrepancies in the evidence have been reconciled. It may further be pointed out that the comparison of these bimodal-incidence curves and the curves obtained by growing plants in culture media at different *p*H values is not a happy one. The growth curves *may* show a bimodal form when expressed graphically—but there is no sort of agreement between the results of different investigators or even the same investigator (**1**, **2**), either as to the existence of a bimodal curve, or as to the points at which maxima occur.

The comparison between the incidence curves and the results obtained by Robbins (**13**) for the swelling curve of potato is equally unfortunate. Apart from the fact that the depression in Robbins' swelling curve occurs at a different *p*H value from that in the incidence curve, the most cursory examina-

tion of Robbins' data shows that he has ignored any other depressions in the swelling curve which did not occur in the region *p*H 5·5–6·0. Swelling curves for plant tissues in relation to different hydrogen ion concentrations are, in fact, composed of a series of "modes" and depressions. At least four depressions exist in the potato swelling curve (**12**), and other tissues examined are essentially similar. It is, therefore, not permissible to institute any comparisons between these curves and bimodal incidence curves.

The above analysis of the evidence may serve to draw attention to three main problems which require consideration:

(i) *Soil acidity* appears to be distinct from *soil sourness.*

(ii) A variety of factors may prevent normal plants from growing on sour and acid soils.

(iii) Data grouped as "incidence" curves require detailed analysis before general conclusions can be based on them. (This would appear to be true of all such data where the distribution ranges overlap.)

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REVIEWS

TREE MYCORRHIZA

Melin, Elias. *Untersuchungen über die Bedeutung der Baummykorrhiza.* Eine ökologische-physiologische Studie. Gustav Fischer, Jena: 1925. Pp. vi + 152 and 48 figures in the text.

Melin's researches on the mycorrhiza of pine, spruce, larch, birch and aspen (Melin, 1921, 1922, 1923, 1924) marked the beginning of a new period in our knowledge of tree mycorrhiza, and already constitute a substantial contribution towards the solution of a much discussed and highly controversial aspect of the mycorrhiza problem. The indebtedness of foresters and botanists to their Swedish colleague is increased by the publication of the papers now under review, in which fresh light is thrown upon the physiology of mycorrhiza in forest trees.

Summarising his earlier work on the mycorrhizal fungi of Conifers, Melin adds the names of several Hymenomycetes to the list of those already identified experimentally as mycorrhiza-formers in pine and spruce, viz. *Amanita muscaria, Cortinarius muscosus, Lactarius deliciosus*, and *Russula fragilis* on pine; and *Amanita muscaria, Cortinarius balteatus*, and *Lactarius deliciosus* on spruce.

He offers also a warning on the need for caution in drawing conclusions from negative results in artificial cultures by reason of the changes known to be induced in the root-fungi under these conditions. He had shown in an earlier paper that the production of mycorrhiza in trees is determined by the physiological states of both symbionts, that of the fungus being especially prone to variation in respect to the qualities which determine "virulence." Accepting this view, the formation of mycorrhiza in Conifers is a "reciprocal phenomenon," a conclusion in agreement with that recently put forward in respect to heather (Rayner, 1924).

The greater part of the present paper is concerned with the results of a long series of experimental cultures designed to investigate the nutrition of both symbionts in Conifers-mycorrhiza and throw light upon their mutual relations.

The conclusions already reached by the author himself are clear from his earlier works. Thus: "Die Birken- und Espenmykorrhiza ist kein parasitisches Gebilde, wie es z. B. McDougall meint, sondern Pilz und Wurzel leben in mutualistischer Symbiose miteinander" (Melin, 1923, p. 517); and, again, after summarising the case for a mutual relation in pine and spruce under conditions favourable to mycorrhiza formation: "Diese optimal entwickelte Mykorrhiza ist u. a. auf gutem Rohhumus und auf zur Aufforstung dränierten Moorböden schön vertreten. Ist der Pilz hier Parasit an der Wurzel oder leben beide in mutualistischer Symbiose zusammen? Auf diese Frage gibt es nur eine Antwort: Wurzel und Pilz leben in mutualistischer Symbiose" (Melin, 1923).

Experimental evidence in support of these views has been obtained from the behaviour of the root fungi and their hosts when supplied with various nutrients and is marshalled in the paper now under consideration. It relates especially to the following aspects of the problem: (1) the general reactions shown by the two symbionts under pure culture conditions, with special reference to nitrogen assimilation; (2) the application of these experimental results to the conditions found in nature.

1. The technique adopted for growing seedlings in pure culture with and without infection was simple and effective. For synthetic cultures the use of sand watered with a suitable nutrient was preferred to humus, owing to the toxicity of sterilised humus to the mycorrhizal fungi; under experimental conditions mycorrhizae were formed only in sand cultures.

Under pure culture conditions, the root fungi of pine and spruce display great variability in growth on favourable media. Some, e.g. the species of *Boletus* associated with pine, are relatively vigorous, others make very feeble growth or are maintained with difficulty in artificial cultures.

As compared with indifferent species and casual soil fungi, they are more easily affected by changes in the substratum and are extremely sensitive to the H-ion concentration of the medium. Whereas the former grow indifferently over a wide range of pH values, the root fungi, with few exceptions, prefer an acid substratum, and are incapable of growth at pH values on the alkaline side of neutrality. Optimum conditions for the fungi of pine and fir are provided by pH values between 4·0 and 5·0. In this connection it is of interest to note that pH values about 4·0 have been recorded for the humus layers of coniferous woods throughout middle and northern Europe by Hesselman (1917), and that Brenner (1924) found pH values ranging from 3·5 to 4·8 in similar soils in Finland.

Of particular interest is the reaction shown to small amounts of phosphates by these fungi, in view of Hansteen-Cranner's (1922) observations on the giving off of these substances by the roots of the higher plants under certain conditions. In Melin's experiments, growth was markedly stimulated when the fungi were brought from pure culture into contact with seeds and seedlings of pine and spruce.

Melin was satisfied that the effect was due to excreted phosphates, and attaches great importance to these observations by reason of the special growth relations shown by the mycorrhizal fungi in nature.

The behaviour of these fungi in relation to nitrogen assimilation is of special importance. No evidence whatever was obtained that any of the forms can utilise atmospheric nitrogen; salts of ammonia, urea and nucleic acid all serve well as sources of nitrogen, while individual fungi can make use of peptone, asparagin, and a number of other organic compounds with equally good results.

A long series of experiments with various carbon compounds led to the conclusion that growth was satisfactory only when glucose was supplied, thus supporting the popular belief that mycorrhizal fungi obtain supplies of carbon from the root cells of their hosts. Direct experiments on the utilisation of the organic compounds in humus were limited by the toxicity of this material when sterilised by heat, but humus extracts freed from micro-organisms by filtering gave weak growth, and the addition of glucose produced vigorous development as on favourable soil.

The reaction of pine and spruce seedlings to various nutrients in pure culture was tested by germinating sterilised seeds, and growing the resulting seedlings in sand and humus cultures in special culture flasks for periods of two to three years. The capacity of such seedlings for independent growth had been determined in earlier experiments (Melin, 1923). Compared with uninfected seedlings they exhibit characteristic structural features in the root systems and have incidentally provided proof that there is no obligate relation with the root fungi, such as occurs in the developmental stages of orchids and heaths.

A series of experiments designed to test the reaction of these seedlings to possible sources of nitrogen led to the following conclusions. There is no fixation of free nitrogen; inorganic compounds of nitrogen, e.g. potassium nitrate and ammonium chloride, provide

suitable sources of nitrogen; simple organic compounds, e.g. asparagin, can be readily utilised; more complex compounds, such as peptone and nucleic acid, are used with difficulty, as evidenced by the excessive length of roots in cultures to which they were supplied.

Similar seedlings of pine and spruce, after inoculation by appropriate root fungi, produced typical mycorrhiza in sand culture. Experiments with various nutrients confirmed the conclusions indicated by the behaviour of fungi and seedlings when growing alone.

In view of its great importance, the possibility of nitrogen-fixation by the mycorrhiza in synthetic cultures was carefully tested and gave negative results, the small increase in nitrogen content at the close of the experiments being regarded as due to atmospheric impurities.

The reaction shown by these synthetic seedlings to various compounds of nitrogen is specially important in view of the long controversy about nutrition in mycorrhizae and their relation to the soil humus.

The comparative growth of cultures supplied respectively with ammonium chloride, peptone and nucleic acid was determined by dry weight estimations, and the figures obtained after three years' growth are supplied in Table 41 of the present paper. Evidence of the general condition of the cultures is provided by photographs of the seedlings after removal from the culture flasks, and is particularly impressive in the case of the nucleic acid cultures (pp. 82, 83). The roots of the seedlings with mycorrhiza are one-third, or less than one-third, as long as those of uninfected control seedlings, and exhibit none of the characteristic symptoms of nitrogen starvation shown by the latter.

When combined with evidence drawn from the figures supplied in the tables, these observations appear to justify Melin's main conclusion: "Diese Versuche zeigen, dass die Mykorrhizen auf komplizierteren organischen Stickstoffverbindungen, beispielsweise Nukleinsäure und Pepton, für die Pflänzchen nützliche Gebilde sind. In Reinkulturen vermitteln nämlich die Mykorrhizen den Pflänzchen die Aufnahme der erwähnten N-Verbindungen im grossen und ganzen leichter, als dies die Wurzeln allein tun kann."

2. The application of these experimental results to conditions found in nature is of particular interest in view of the controversial views expressed by earlier workers, in respect to the significance of mycorrhiza in forest trees.

Observations on the H-ion concentration most favourable to the root fungi have been supplemented by field observations, as mentioned above, and become significant when it is realised that it is only in humus soils of the more acid type that coniferous mycorrhiza is freely formed in nature. Moreover, it is in soils of this class, i.e. those consisting largely of raw humus (Rohhumusböden), that the nitrogen supply exists chiefly in the form of organic compounds of relatively complex type.

In humus soils with a more neutral reaction (Mullböden), e.g. those of heaths, coniferous mycorrhiza only appears sporadically, and it is suggested by Melin that its formation may be directly related to the known differences of behaviour in such soils in respect to the breakdown of organic material and the rate of nitrification.

With regard to the distribution of the mycorrhizal fungi in nature, great importance is attached by Melin to the supply of phosphates associated with roots. It is suggested that these substances may be indispensable to the fungi, perhaps for the production of fruit bodies, perhaps in relation to the germination of spores.

The main contention in this paper, namely, that mycorrhiza possesses a vital significance for trees and other plants growing in acid humus, if correct, opens up a whole new field for experimental enquiry, since it becomes of the first importance to provide conditions favourable to the formation and active functioning of mycorrhiza. This is especially true

in relation to forestry, since in woodland soils the amount of humus present is constantly increased by the process of leaf fall.

In a summarised account, it is not easy to do justice to the wealth of observation and experiment that have made the publication of this paper possible. Its value is greatly enhanced by the large number of tables supplied in the appendix, in which the author's experimental results are clearly set out.

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M. C. RAYNER.

SOUTH AFRICAN PLANT FORMS

Bews, J. W. *Plant Forms and their Evolution in South Africa.* London, 1925. Pp. 199, 31 figures and 1 map.

The flora of South Africa has been long regarded as being one of very great interest from many points of view, and not least from the fact that it contains two very widely separated elements. The one, and to botanists outside, probably the better known, occupies a rather restricted area in the south-west portion; the other is much the more widespread flora and occupies the central and eastern portions.

For the study of plant migrations and the possible phylogenetic history of such floras or of any special types of plants, South Africa possesses very many advantages. The continent is a very old and stable one, and the land connection with the tropics and the northern hemisphere has remained unbroken, at any rate from the time of the evolution of the angiosperms. The climate also, although it has undergone fluctuations, has not had any of the violent devastating changes that have taken place in the north. At the present time South Africa exhibits considerable varieties of climate each with its own characteristic vegetation type.

In commencing to trace an evolutionary sequence of plant form and, hence, indirectly, of vegetation types, the author distinguishes two types of habitat. The first are those which have persisted for immense periods of time practically unchanged, what are termed primitive types of habitat. These are claimed to have remained unchanged since the evolution of flowering plants. The second are changing or derivative types of habitat which have not this long unchanged history. The former are represented by moist tropical or subtropical forest, marshes or swamps, stream sides, sea shores, and possibly mountain tops. The vegetation in all these cases is very widespread and covers very wide geographical areas without change of type. It is in these primitive habitats that the most ancient growth forms are looked for. In determining on these, use is made of confirmatory evidence from other sources, such as floral morphology, structure and so on. The most primitive forms are regarded as being represented by the tree with broad simple leaves and by the halophyte.

All other types are derivatives and have been evolved in relation to increasing aridity. Evolution of growth form is regarded as being a progression from the hygrophyte towards the xerophyte. Extreme xerophyte desert plants, succulents, etc., represent very modern forms. The annual is regarded as the most highly evolved growth form. Certain plants, e.g. Gymnosperms, are considered on a different basis; these plants, very few in number in South Africa, are looked on as possible relics from a pre-angiosperm flora.

Accepting this scheme of evolution of growth form, the author argues that succession passes through a series of stages that are the reverse of those passed in the evolution. The succession series is utilised in the building up of the phylogenetic story of the flora: statistics of growth forms, numbers of genera and species and so on are quoted in support of the theory advanced.

These premises form the basis for the sketch of the origin and migrations of the flora. That of the east and the central region is regarded as having come from migrations of plants from the tropics and subtropics. Here a good and connected argument is advanced in support. This is the author's own ground and the account here is much more living than other portions of the book.

A special chapter is devoted to the origin and establishment of grassland which forms such an important part of the South African vegetation. It is claimed that the evolution of the grass-like plant enabled the angiosperm flora to occupy vast areas that previously it could not penetrate. The impression left with the reader, however, after reading this chapter, is that this exceedingly perplexing question has not been advanced towards solution.

The chapters on the Karroo and Deserts and on the south-west flora are much less happy than the earlier ones, and cannot be said to advance our knowledge of the flora to any appreciable extent. As regards the last, the author does not commit himself definitely to either of the prevailing views as to its status, though he inclines perhaps towards origin by mountain range migration from the north. While emphasis is laid on the penetration of eastern and Karroo genera and species into this flora, the reverse is not mentioned; but surely such a genus as *Pelargonium*, for example, with a few specialised Karroo species and a large number, often with much less highly evolved growth forms, in the south-west, might be regarded quite as fairly as showing a north-east migration. All through, however, there seems to be a tendency, perhaps inevitable, to select and weight the desirable evidence, and several statements are made that seem to need much in the way of proof before they can be accepted. As a result few will feel inclined to accept all the author's statements and conclusions.

Reading this book, one cannot help feeling that the interest falls off in the later parts. While dealing with the eastern portions of South Africa, Prof. Bews gives the impression of feeling fully at home, whereas his account of the more western portions, being drawn largely from second-hand information, is much less convincing.

While the book deals exclusively with the flora of South Africa, there is much, especially in the earlier chapters, that is of general interest. The book should certainly serve to stimulate interest in an intricate but very fascinating side of ecological study.

A bibliography of works relating to the South African flora is given and the book has a full index.

R. S. A.

BRITISH ECOLOGICAL SOCIETY

SUMMER EXCURSION 1925

The summer field meeting was held at Aberystwyth where 17 members and some visitors assembled on August 10. The Headquarters were at the Alexandra Hall of Residence where most of the party were accommodated. A very interesting week was spent, in spite of somewhat unfavourable weather, under the guidance of Prof. Stapledon and Prof. Lloyd Williams.

On the first evening a meeting was held at which Prof. Stapledon gave an account of the work of the Welsh Plant Breeding Station and its relation to some of the ecological problems of the district. Much of the mountain area inland from Aberystwyth is covered with grasslands which are heavily grazed by sheep, and it is important to ascertain the effects of constant grazing on different species and varieties of grasses. The methods of investigation and some of the results were described. Other branches of the work of the station were described including the production of new races of grasses, cereals and clovers by hybridisation, and the study of the effects of altering the normal period of daily illumination on different plants. Prof. Lloyd Williams gave an account of some features of interest in the vegetation of the district and of the mode of occurrence of the chief woodland types in the area.

The first day was spent in visits to the Plant Breeding Station, where many things of interest were seen. Mr Tincker demonstrated some of his experiments on the effects of illumination (cf. *Annals of Botany*, 1925) and showed how considerable were the results of growing plants in conditions under which they were exposed to sunlight for a shorter period than that of the normal day. This treatment affected the habit of the plants, their time of flowering and their carbohydrate content. Experimental plots containing clover and cereal hybrids were visited and experiments on the grazing and cutting of grasses were demonstrated.

On the second day the party paid a visit to Plynlimmon with the intention of studying the types of grassland of that district. Most of the observations made, however, related to the climatic conditions of the region as members had full opportunity of realising the exposure of these slopes to wind and the amount of rainfall which may occur on a summer's day.

The wooded valleys between the uplands and the coast were next visited under the guidance of Prof. Lloyd Williams. Most of these were probably covered at one time with *Quercus sessiliflora* woods, though *Quercus robur* woods are found in a few places. In several localities the effects of recent felling were observed. In some places the oaks were growing up from the old stools, while in others the steep hillsides appeared to have become almost bare of vegetation. An interesting case was pointed out where an area seemed to be in process of invasion by *Ulex*. The route taken was up a valley containing several old lead mines and the poisonous effects of the small traces of lead salts in the drainage water were very noticeable. Not only were algae and aquatic plants almost absent from the main river but the colonisation by plants of the recent deposits and gravels seemed to be greatly retarded. The beautiful oak woods at the Devil's Bridge were found to be very interesting. They cover the steep sides of narrow valleys and being very moist they possess a very large and varied cryptogamic flora. Large tufts of *Polypodium vulgare* with many mosses and liverworts growing epiphytically on the trees were conspicuous features, and several of the less common species of British ferns were seen.

The last excursion was to the great Borth bog and to the salt marshes of the Dovey estuary. Parts of this area have been already described (Yapp and Johns in this JOURNAL, 5, 1917 and **10**, 1922), but other interesting features were also seen. A brief period was spent on the bog, where the three British Droseras were collected. The changes in the vegetation due to peat digging and the subsequent succession were noted. After visiting the salt marshes, the party proceeded to the great shingle bank at the mouth of the estuary where traces of the old hooks or lateral banks were pointed out on the golf links. Near this point an interesting isolated pool was shown to the members and the zonation of its vegetation explained, it contains in one place a vigorous growth of a Chara, a plant type which is very rare in the neighbourhood.

During the four days devoted to excursions many varied and interesting types of vegetation were seen and a considerably longer period might have been profitably devoted to their examination. It is hoped however that in the near future further studies on the vegetation of the district will be published by the members of the University of Wales connected with the Botanical and Agricultural departments at Aberystwyth.

H. H. T.

ANNUAL MEETING, MANCHESTER, 1926

The 12th Annual Meeting was held in the Botanical Department of the University, Manchester, on January 9th, 1926. The President, Prof. F. E. Weiss, occupied the Chair.

After the minutes of the previous Annual Meeting had been read and confirmed the President read a letter from Prof. Schroeter in which he expressed his great appreciation of the action of the Society in electing him an Honorary member.

The Treasurer then presented the accounts for 1925 (p. 171), and pointed out that the favourable financial position, by far the most favourable in the history of the Society, was largely due to the great increase in the sales of back numbers and that the year's expenses were not covered by members' subscriptions and sales of the *current volume* of the Journal. The large receipts from the sales of back volumes really represented realisation of capital assets. On the proposition of Prof. Thoday seconded by Dr Woodhead the accounts were formally adoped.

A hearty vote of thanks was accorded to Mr Paulson for auditing the accounts and by a unanimous vote he was elected auditor for the ensuing year. A hearty vote of thanks was also accorded Mr Boyd Watt for his admirable conduct of the finances of the Society.

The Hon. Secretary then submitted his Report, which was adopted.

HON. SECRETARY'S REPORT FOR THE YEAR 1925

During the past twelve months three meetings of the Society have been held. The Annual Meeting took place at University College, London on January the 10th and was preceded by a Soirée in the Botanical Department of which an account has already appeared in our Journal.

The chief Field Meeting was held at Aberystwyth from August 10th–15th under the able guidance of Prof. Lloyd Williams and Prof. Stapledon to both of whom the Society is indebted for the admirable arrangements for the comfort of those who took part. The annual Foray in conjunction with the Mycological Society was held at Burnham Beeches, and for the conduct of this we were again indebted to Mr Ramsbottom.

Two numbers of the Journal have been issued during the year, in February and September respectively, together comprising 336 pages and 14 plates. This it may be pointed out is a larger total than when the Journal was issued in four parts and indeed is nearly equal in size to the issue of last year, for which a special donation was received. It should therefore

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR 1925

Income

	£ s. d.	£ s. d
Subscriptions received including arrears	189 6 0	
Less prepayments and repayment	8 15 0	
		180 11 0
Interest on Bank Deposit		3 6 5
Sales of Reprints		10 11
Journal of Ecology—Sales, etc.:		
Current volume, No. XIII, 1925 ...	303 17 6	
Back volumes and parts	266 17 11	
Advertisements	3 0 2	
		573 15 7
		758 3 11

Expenditure

	£ s. d.	£ s. d
Working Expenses:		
Postages and Stationery	2 5 6	
Printing	2 12 0	
Bank Charges	15 8	
Expenses of Soirée	11 18 10	
		17 12 0
Journal of Ecology:		
Paper, Printing and Illustrations ...	476 7 2	
Binding	14 13 0	
Postages and Advertising	24 17 10	
Insurance of Stock	2 6 7	
Publishers' Commission	74 10 9	
		592 15 4
		610 7 4
Balance—Surplus on Year carried to Balance Sheet		147 16 7
		758 3 11

BALANCE SHEET AT 31ST DECEMBER, 1925

Liabilities

	£ s. d.	£ s. d.
Subscriptions prepaid for 1926		7 10 0
General Revenue Account—Balances		
Surplus at 31st December, 1924 ...	93 2 10	
Surplus from Revenue Account, 1925	147 16 7	
		240 19 5
		248 9 5

Assets

	£ s. d.	£ s. d.
Westminster Bank—Credit Balances:		
Current Account	24 4 8	
Deposit Account	220 0 0	
		244 4 8
Journal of Ecology:		
Credit Note from Publishers		4 4 9
NOTE. A further asset is the unsold stock of the *Journal of Ecology* held for the Society by the Publishers.		
		248 9 5

HUGH BOYD WATT,
Hon. Treasurer.

I have examined the accounts for the year ending 31st December, 1925, and certify them to be a correct statement and that all vouchers are in accordance with the receipts and payments shown therein.

be a matter for gratification to members that whilst the Council deem it necessary to raise the price to non-members in conformity with the actual cost of production, it is still possible to supply the Journal to members without raising the subscription and, so far as the Council can foresee, that necessity is not likely to arise.

We regret to have to record the loss by death of three of our members. Miss Winifred Smith, who endeared herself to all those with whom she came in contact, is a loss that will be keenly felt by many, and particularly by her colleagues at University College, London, of which she was Tutor to women students. Mr Frank Morey, who, like Miss Smith, joined the Society at its inception, was one of that rapidly disappearing class of naturalists whose knowledge and sympathies embrace most branches of Field Natural History. He was the founder and mainstay of the Isle of Wight Natural History Society, to which his loss is an irreparable misfortune, but he has left a permanent memorial of his work in the Island, in his *Natural History of the Isle of Wight.* Mr L. W. Cole, whose untimely death occurred in the early part of the year, was an ecologist of some promise who collaborated in a study of the vegetation of English Heaths, part of the results of which have been published in our Journal.

Five members have tendered their resignations but we welcome in their stead nineteen others who have joined since our last Annual Meeting. The membership is now 166 ordinary members and three Honorary members.

Further Rise in Price of the Journal of Ecology

The President then moved from the Chair the Council's recommendation that the cost of the Journal to non-members should be raised to 30*s*. Dr Watson spoke against the motion, which he thought would affect foreign subscriptions adversely. Dr Salisbury called attention to the fact that the cost of production of the Journal was in excess of the income derived from the sale of the current volume, and it was therefore only fair that non-members should contribute in money in place of the personal service contributed by members. The motion was then put to the meeting and was carried with one dissentient vote.

Election of Officers, etc.

The Meeting then proceeded to the election of Officers as follows:

President: Dr Woodhead.
Vice-President: Dr H. Hamshaw Thomas.
Council Members: Prof. Bews, Mr Ramsbottom, Prof. Yapp.
Hon. Editor: Mr Tansley.
Hon. Secretary: Dr Salisbury.

The following were elected members:

Mrs Bacon, Miss Gertrude Connolly, Dr G. Jessop, Mr F. S. Laughton and Mr J. Rees.

Scientific Proceedings

Dr W. G. Smith then communicated a paper on the Improvement of Hill Pasture, in the course of which he drew attention to the effect of burning as an amelioration rather than as a permanent improvement and the comparative permanence of the burn limits. The distribution of *Juniperus* on the area in question was attributed to the freedom from fire of the areas where this plant is present. The effects of various manurial treatments were described.

Miss V. E. L. Anderson dealt with some aspects of the Water relations of the Vegetation of the Chalk. The natural water content of the soil of a Chalk Down had been determined at four successive levels at intervals of a fortnight or less throughout a period of eighteen months, which included one year of exceptionally high rainfall and also a period of prolonged drought. The water content was found to have an average value of 36·7 % at the surface and 27·2 % at a depth of 2 ft. 6 ins. The extreme values for the surface were 61·2 % and 8·58 %. The relations of the water content to meteorological and soil conditions were dealt with and the results of a study of the depth and extent of the root systems of the chalk flora were briefly outlined. Whilst a number of species, such as *Polygala vulgaris*, are shallow rooting the root systems of *Poterium sanguisorba* and other of the perennials may attain a depth of over 33 ins.

Mr O. W. Richards read a paper on Animal and Plant Habitats in which he emphasised the difficulty of correlating the communities of animals and plants. The plant community embraced a complex of animal habitats and extensive subdivision of the former was necessary before any clear relation between the two could be established. Owing to the "food cycle" of animals the presence of a species depended not only on the conditions favourable for itself directly but on those favourable to its source of food. Animals were therefore regarded as occupying "niches" rather than habitats.

Mr S. K. Mukerje gave an account of the plant communities found in the Kashmir Himalayas between 5000 and 18,000 ft. Several of the communities described were similar to those of Britain, such as the Phragmitetum, Scirpetum, Typhetum and Fen. The differentiation of these aquatic communities was regarded as depending chiefly upon the depth and translucency of the water and upon the degree of sedimentation. The Xerarch and Hydrarch successions culminate in a mesophytic community dominated by *Cedrus deodara*. Above this latter, which attains to 8000 ft., forests of *Abies webbiana* and *Betula utilis* are followed by Juniper scrub and alpine pasture.

Dr Woodhead described the results of examinations of peat made recently in the Pennines which showed that the peat was already being formed in late Neolithic times. The Roman remains rest on a considerable deposit of peat whilst above these peat of considerable thickness has been formed.

The last paper was a communication of Prof. Oliver in which he described the extensive area at the mouth of the Havre colonised by *Spartina Townsendii*. The chief feature of interest is that the *Spartina* is here followed by *Glyceria maritima*, the first recorded example of a succession initiated by the Rice grass.

The meeting terminated with a hearty vote of thanks to Prof. Weiss and his colleagues for their hospitality and for arranging the exhibition the previous evening.

LIST OF MEMBERS (9 JANUARY, 1926)

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, Dr E. J. SALISBURY, The Briars, Crosspath, Radlett, Herts.

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VOLUME XIV AUGUST, 1926 No. 2

SPHAGNUM BOGS OF CENTRAL RUSSIA: PHYTO-SOCIOLOGY, ECOLOGY AND SUCCESSION

BY N. J. KATZ.

(*With five Figures in the Text.*)

CONTENTS.

PREFACE

The data presented in this paper were obtained by my researches in the Governments of Moscow (district of Bogorodsk and Dmitrov), Wladimir (district of Wladimir) and Ivanovo-Voznessensk (districts of Teikof, Sereda, Ivanovo-Voznessensk and Shouja). The total area of the Sphagnum bogs investigated exceeded 400 sq. km. The scanty literary material concerning the former Government of Riazan[1] (**1**) and that of Tver (**2**, **3**), as well as information directly obtained from A. J. Bronzoff about the former Government of Jaroslav (now Rybinsk) points to a complete analogy between the Sphagnum bogs of these provinces and those I visited myself. It is thus highly probable, that the information given in this paper is also applicable to the greater part of that vast region of Middle Russia which, according to P. Maievsky (**4**),

[1] This part of the Government of Riazan has now been joined to the Government of Moscow.

extends over the following Governments[1]: Moscow, Tver, Jaroslav, Kostroma, Wladimir, Nijni-Novgorod, Riazan, Kaluga, Smolensk, Orel and Penza. Only a few communities of northern plants (*Empetrum nigrum*, *Rubus chamaemorus*, and a few others) belong exclusively to the northern part of this region and are not found in the south. The immense majority belong to the Sphagnum bogs of the whole region, except perhaps those of Orel and Smolensk.

My investigations were made in 1917–21. The results have as yet been published in part only (in Russian), (**5**), (**6**), (**7**), (**8**).

INTRODUCTION

Rübel (**9**) distinguishes four branches of the study of vegetation:

(1) Isolation of plant communities and the study of their constitution (Gesellschaftsmorphologie).
(2) Distribution of communities in space (Chorologische Soziologie).
(3) Ecology of communities (Ecologische Soziologie).
(4) Succession of communities (Genetische Soziologie).

To me it seems that no study of the ecology of communities is possible without a knowledge of the ecology of the species which form them, so that questions touching the ecology of species will here take a prominent place.

If we exclude researches which are antiquated in method and give only disjointed and by no means typical lists of species, and also those which touch mainly on palaeontological and stratigraphical questions, there remain very few monographs (**1, 2**) which contain accounts of the origin and stratigraphical structure of the bogs, of the botanical and chemical composition of the peat, and give descriptions of the vegetation. There does not yet exist in Russian botanical literature any list of the principal plant communities of the Sphagnum bogs of Central Russia, much less anything approaching a complete characterisation of these communities.

I shall therefore endeavour, by synthesising the description of various observed plots, to define, for the first time, these communities and to enumerate the species which characterise them. It is also necessary to describe the situations of the communities on the bog surface and the relative areas they occupy (Fig. 1). It was impossible in the time at my disposal to employ exact methods such as "Linientaxering," as used by the Swedish botanist Thore Fries for instance (see H. Osvald, **11**), and I have therefore made an approximate estimation of the relative surfaces occupied by the different communities, as shown in the diagram.

The ecology of the bog species, as I understand it, has scarcely been studied at all, either in the region dealt with here, or in Russia generally. The observations of D. A. Gerassimoff (**1, 2**) concern only a few bogs, i.e. they were made on a comparatively small area. Exact knowledge of the ecological

[1] It is unnecessary to deal with the southern and south-eastern Governments of this part of Russia since hardly any Sphagnum bogs occur in them.

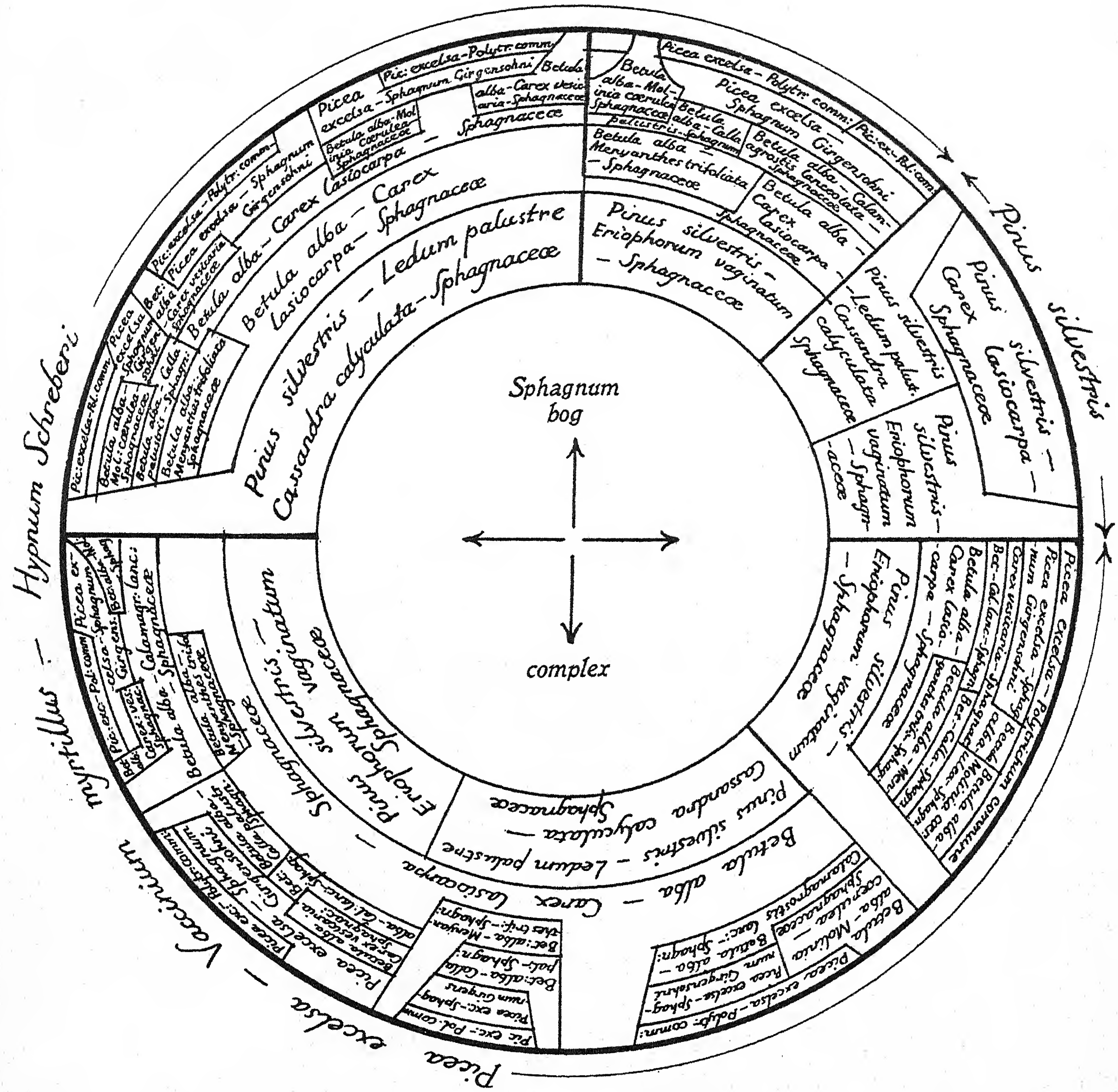

FIG. 1. Diagram illustrating the arrangement of associations of a Sphagnum bog developing in the midst of spruce and pine forest. The central space represents the Sphagnum bog complex (see text), the arrows indicating the centrifugal march of the associations, which gradually encroach on the forest. The peripheral sectors represent the different associations of the succession from untouched forest to the Sphagnum complex. Their areas are roughly proportional to the areas of the different seral associations. One octant represents the succession from pine forest, the remaining seven from spruce forest. It can be seen that the former succession is shorter than the latter, which varies in length, sometimes passing through only two, but often through as many as six stages.

adaptability of species can only be obtained by an examination of extensive material over a wide area.

Again, while the altitudinal zonation, as shown by the microrelief, of the plant communities of meadowland has long been studied in Russia, and is now worked out very minutely (**12**), the same phenomenon and its relation to the ecology of the bog plant communities of Central Russia have scarcely attracted the attention of investigators, though they represent an important and interesting chapter of phytosociology. My application of the method of "ecological analysis" is also the first in Russian literature, and I am unaware if anything of the kind has been done in other countries.

Likewise the succession of vegetation on the bogs of Central Russia has been but little studied, though Soukacheff (**13**), Abolin (**14**), and others have investigated the bogs of north-western Russia from this point of view. The subject has very little in common with botanical researches upon the composition (nature) of peat, which usually give but a schematic picture of the way in which certain types of bog succeed others.

Finally little is known of the varied effects of culture on bog vegetation.

In this paper an attempt has been made to make good these deficiencies so far as was possible during a superficial survey of great areas of bogland, which left no time for the application of exact methods of evaluation of habitat factors. The vegetation is described in terms of the small communities called *associations* by the Upsala school of phytosociologists (Du Rietz, **15**), as has already been done by H. Osvald (**11**) for the Sphagnum bog vegetation in Sweden, and the term has been used in this sense throughout the paper[1]. My descriptions refer to separate plots of the different associations, but not to quadrats of definite size, as used for instance by the Upsala school (**15**). The species are arranged according to the strata (Schichten) of the community, beginning with the uppermost. The life forms adopted are as follows:

md Deciduimagnolignosa (deciduous trees more than 2 metres high).
ma Aciculimagnolignosa (needle-leaved trees).
p Parvolignosa (woody plants from ·8 to 2 m. high).
n Nanolignosa (undershrubs below ·8 m.).
h Herbaceous plants of non-gramineous type.
g Grasses and other plants, such as sedges, of gramineous type.
b Leafy mosses and liverworts.
s Sphagna.
l Lichens.

Degrees of abundance are designated according to Drude's scale. Associations are named according to the dominants of the different strata of the association, and designated by the initial letters of the names of these dominants. In characterising the three fundamental types (Marsh or Fen,

[1] It should be noted that this use of the term 'association' is quite different from that current in most countries, where it is applied to a much larger unit. [Ed.—JOURNAL OF ECOLOGY.]

Niedermoor, Transition bog, *Uebergangsmoor*, and Sphagnum bog, *Hochmoor*) the vegetation itself has been considered first of all, rather than the factors of the habitat (chemical composition of water), or the general aspect (character of bog surface).

The three principal types may be characterised as follows:

1. MARSH or FEN (*Niedermoor*). Dominant and characteristic species: *Alnus glutinosa*, *Betula alba*[1], *Carex caespitosa*, *C. paradoxa*, *C. diandra*, *Aulacomnium palustre*, *Drepanocladus vernicosus*, *Camptothecium nitens*, *Acrocladium cuspidatum*. Sphagna absent or rare. This type chiefly occurs in the river valleys and is fed by ground water rich in mineral salts.

2. TRANSITION BOG (*Uebergangsmoor*). Dominant and characteristic species: *Betula alba* (more rarely *Pinus silvestris*), *Carex lasiocarpa*, *Calamagrostis lanceolata*. Sphagna (chiefly *S. recurvum* (P.B.) Warnst. and *S. subbicolor* Hampe) form a more or less continuous carpet. The type occurs on the edges of Sphagnum bogs or develops in place of (1) along the upper courses of rivers. Water less rich in salts than in (1), partly ground, partly aerial water.

3. SPHAGNUM BOG *sensu stricto* (Hochmoor). Dominant and characteristic species: *Pinus silvestris*, *Cassandra calyculata*, *Ledum palustre*, *Andromeda polifolia*, *Eriophorum vaginatum*, *Rhynchospora alba*, *Scheuchzeria palustris*. The dominant Sphagna are *S. medium* Limpr., *S. recurvum*, *S. balticum* Russ. The type is situated on watersheds and the bog water is poor in salts, being fed by atmospheric water.

1. ECOLOGY OF SPECIES AND OF ASSOCIATIONS

If the quantities of any habitat factor (e.g. distance below the surface of the ground water) are represented as abscissae, and the quantities of a species (e.g. weight developed on a unit area) as ordinates, a curve representing the relation of the species to the given factor (curve of adaptability) may be drawn, the summit of the curve marking the optimum condition of the given factor for the species. If we limit the application to dominant species, it is evident that the range of conditions in which a given species is dominant (amplitude of dominance) is much narrower than the range for isolated individuals (amplitude of occurrence). Here we are chiefly concerned with amplitude of dominance.

The curve of adaptability of a species to a given factor may be modified (*a*) by the part of the species area under consideration, (*b*) by the particular complex of environmental factors, (*c*) by competition.

The researches carried out by myself and S. V. Katz in 1924 on the Tatitschevskoe marsh (Dmitrov district, Gov. of Moscow) show that *Menyanthes trifoliata* is dominant with a ground water depth of 10 to 70 cm., *Carex rostrata*

[1] The name *Betula alba* is used throughout in the aggregate sense. The common form, everywhere dominant in the bog birch forests, is *B. pubescens*; *B. verrucosa* is occasional only.

15–35 cm., *C. limosa* 10–20 cm., *Aulacomnium palustre* 35–60 cm., *Camptothecium nitens* 18–32 cm., *Drepanocladus vernicosus* 10–20 cm. This makes it clear that *Menyanthus* can form communities with all three species of moss mentioned, *Carex rostrata* only with the two latter, and *C. limosa* only with the last, and this is confirmed by study of the communities in nature. Fig. 2 illustrates this. On the horizontal base line are marked the depths of the ground water below the surface, the other horizontal lines (whose varying heights represent the strata of the species) showing the amplitudes in respect of this factor of the six species mentioned. The vertical lines mark the limits of the amplitudes of adaptation of the "associations."

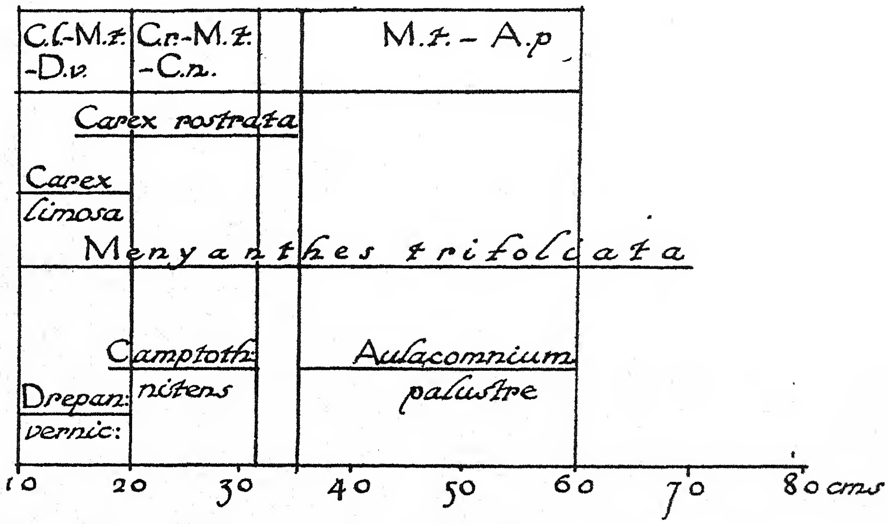

FIG. 2. Diagram showing amplitudes of dominance of certain species and associations with respect to depths of ground water. The top line shows the associations.

Thus the quantitative study of the ecology of species explains, in a general way, why a given species combines in an association with a second species and not with a third, and shows that the ecology of an association, the amplitude of its adaptability, depends in the first place on the ecology of the species constituting it (at least so far as bog associations are concerned). Finally, the amplitude of adaptability of species explains in great measure their capacity for participating in a greater or smaller number of associations.

An ecologist possessing enough quantitative data could foretell, with sufficient probability, the possible combinations of species in associations, and the main lines of their composition and ecology[1]. The establishment of quantitative ecological characterisations is work of the future, but even com-

[1] There is good ground for believing that the mutual action of plants upon one another has but a secondary importance in the constitution of bog plant associations. The habitat factors, which group into associations species with a definite amplitude of adaptability, are decisive. I possess a certain number of data supporting this belief.

parative qualitative characterisations are of value to the phytosociologist. An example will illustrate this. On the Tatischevo marsh *Carex limosa* is dominant in water of 20 (German) degrees of hardness, and rich in iron. On the Sphagnum bogs *C. limosa* is dominant in hollows where the water contains a minimum of CaO and iron. Thus the amplitude of this species in respect of these factors is very wide. But in respect of moisture it is very narrow, for *C. limosa* is dominant only when the depth of the ground water is between 10 and 20 cm. It is thus evident that this species can form an association equally well with *Sphagnum balticum* Russ. in a Sphagnum bog, and with *Drepanocladus vernicosus* in a marsh. Both soils have high water content but the soluble salt content is widely different. A ground water depth of 20 cm. marks the extreme limit for the growth of trees, so that it is easy to understand why *Carex limosa* is not met with in forest bogs.

The study of the ecology of species on these lines also gives us a means of establishing ecological series of associations through the use of *plant indicators*. This method, which I call *ecological analysis* of associations, was first used by myself in conjunction with S. V. Katz on the Tatischevo marsh in 1924 in the analysis of experimental quadrats of definite size. Here it is used for the analysis of separate plots differing in size. I am unaware whether the method has been employed elsewhere in Russia or abroad. *Indicators* are for the most part species with a narrow amplitude of adaptability to a given environmental factor. For "moisture series" it is convenient to employ as indicators, on the one hand, species which inhabit mineral soil, and, on the other, species for which excess of moisture gives optimum conditions. The number of indicators of each group on each plot of the association is counted, and the mean number of indicators for each plot is calculated. If the number of plots be sufficient their difference of size has no effect on the final result. The closer the ecological relationship between the associations studied, the more difficult it becomes to choose the indicators, the more sensitive they must be, and the fewer they will be in number.

2. SPHAGNUM BOG (HOCHMOOR)

A. ASSOCIATIONS.

In Central Russia Sphagnum bogs occupy an enormous area comprising thousands of square kilometres and exceeding that of the Marshes and Transition bogs taken together. In consequence of the small number of species dominant in the Sphagnum bogs, the number of associations is also very limited. Association-complexes[1] have a wide extension, and their vegetation consists of small plots of different composition, a few metres square, and alternating with one another, which represent associations or association-fragments[1]. The distribution of these is connected with the microrelief of the bog, which is very disjointed. There are high tussocks which may be more

[1] Upsala terminology. [Ed.—JOURNAL OF ECOLOGY.]

than 5 m. in diameter, or the elevations may take the form of low ridges running parallel in a certain direction and anastomosing. The width of these ridges does not exceed 2 m., but their length is often great. The higher tussocks and ridges may be 70 cm. above the bog surface, and between are wet hollows. Sometimes the tussocks or ridges have the appearance of islands in a flat swampy bog, sometimes they are so close together that the wet depressions between are like narrow valleys.

The summits of the highest tussocks and ridges are covered by the association *Pinus silvestris-Ledum palustre-Cassandra calyculata*-Sphagnaceae, the sides by *Pinus silvestris-Eriophorum vaginatum*-Sphagnaceae. The hollows are often filled by a mixed association, where *Carex limosa*, *Rhynchospora alba* and *Scheuchzeria palustris* are dominant. Sometimes the vegetation of the hollow is zoned, the outer zone consisting of *C.l.*-Sph., the inner of *Sch.p.*-Sph. Occasionally another association, *Rhynchospora alba*-Sph., occurs between *P.s.-E.v.*-Sph. and *C.l.*-Sph., occupying the peripheral parts of the hollows.

The association-complexes described establish themselves in the centres of the Sphagnum bogs, occupying not less than half the whole area of the Sphagnum and Transition bogs. No detailed description of them exists in Russian literature except in my own papers (**5**, **6**). On the periphery of these association-complexes a uniform vegetation occupies a considerable space. Here we have the associations *P.s.-L.p.-C.c.*-Sph. and *P.s.-E.v.*-Sph., more rarely *C.l.*-Sph.

The following are lists of the species of the associations above mentioned.

The abundance indications follow Drude: *soc.* social, *cop.* copious, *spar.* sparse, *sol.* solitary. The numbers represent percentages of all the plots in which the species occur with the designated abundance.

1. Association *Pinus silvestris-Ledum palustre-Cassandra calyculata*-Sphagnaceae. (Compound list from sixteen separate plots.)

ma. Pinus silvestris cop. 25; spar. 75
Picea excelsa sol. 7
md. Betula alba sol. 25
n. Ledum palustre cop. 31; spar. 62·5; sol. 6·5
Cassandra calyculata cop. 31; spar. 57; sol. 12
Andromeda polifolia sol. 69
Vaccinium uliginosum cop. 6·2; sol. 31·3
V. vitis-idaea sol. 37·5
V. myrtillus sol. 12·5
Rubus chamaemorus spar. 6·2; sol. 6·3
Vaccinium oxycoccus sol. 81·2
V. microcarpum sol. 12·5
h. Drosera rotundifolia sol. 37·5
Melampyrum pratense sol. 6·3
g. Eriophorum vaginatum spar. 44; sol. 44
Rhynchospora alba sol. 12·5
Scheuchzeria palustris sol. 6
b. Hypnum schreberi sol. 25
Polytrichum strictum sol. 25
Dicranum bonjeani sol. 12·5
Aulacomnium palustre sol. 6
s. Sphagnum medium soc. 19; cop. 75; spar. 6
S. recurvum (P.B.) Warnst. soc. 19; cop. 69; spar. 12
S. fuscum sol. 12
S. acutifolium sol. 6
l. Cladonia rangiferina sol. 6

2. Association *Pinus silvestris-Eriophorum vaginatum*-Sphagnaceae. (Compound list from eighteen separate plots.)

ma. Pinus silvestris cop. 17; spar. 28; sol. 33
md. Betula alba sol. 17
n. Cassandra calyculata spar. 11; sol. 83·5
Andromeda polifolia sol. 78
Ledum palustre sol. 44·5
Vaccinium vitis-idaea sol. 17
V. uliginosum sol. 5·5
V. myrtillus sol. 5·5
V. oxycoccus sol. 89
h. Drosera rotundifolia sol. 50
D. obovata sol. 5·5
Orchis maculata sol. 5·5
Melampyrum pratense sol. 5·5
g. Eriophorum vaginatum soc. 11; cop. 64; spar. 25
Scheuchzeria palustris spar. 5·5; sol. 11
Carex limosa sol. 11
C. pauciflora sol. 11
C. rostrata sol. 5·5
C. lasiocarpa sol. 5·5
Rhynchospora alba sol. 5·5
b. Polytrichum strictum sol. 28
Hypnum schreberi sol. 22
s. Sphagnum recurvum (P.B.) Warnst. soc. 28; cop. 50; spar. 16·5; sol. 5·5
S. medium Limpr. soc. 22; cop. 22·5; spar. 22·5; sol. 27·5
S. fuscum cop. 5; sol. 11
S. acutifolium sol. 17

These two associations (1 and 2) occupy two-thirds of the total surface of the Sphagnum bogs: each forms little plots of a few square metres in the complexes: in bogs with uniform vegetation each occupies large areas of hundreds or thousands of square metres.

3. Association *Carex limosa*-Sphagnaceae. (Compound list from eleven separate plots.)

ma. Pinus silvestris sol. 9
Picea excelsa sol. 9
md. Betula alba sol. 9
n. Cassandra calyculata sol. 91
Andromeda polifolia sol. 91
Vaccinium oxycoccus sol. 54·5
Salix myrtilloides sol. 9
h. Drosera anglica sol. 9
Naumburgia thyrsiflora sol. 9
Orchis maculata sol. 9
Menyanthes trifoliata sol. 9
g. Carex limosa cop. 45·5; spar. 54·5
Scheuchzeria palustris spar. 41; sol. 50
Eriophorum vaginatum sol. 54·5
Rhynchospora alba sol. 45·5
Carex rostrata sol. 27
C. lasiocarpa sol. 9
b. Hypnum fluitans sol. 9
Polytrichum strictum sol. 9
s. Sphagnum balticum soc. 100
S. recurvum (P.B.) Warnst. sol. 18
S. medium sol. 18

This association (3) occupies much less space than the two preceding ones.

4. Association *Scheuchzeria palustris*-Sphagnaceae. (Compound list from seven separate plots.)

ma. Pinus silvestris sol. 28·5
md. Betula alba sol. 14
n. Cassandra calyculata sol. 71
Andromeda polifolia sol. 57
Vaccinium oxycoccus sol. 57
h. Drosera rotundifolia sol. 14
D. anglica sol. 14
D. obovata sol. 14
g. Scheuchzeria palustris cop. 50; spar. 50
Eriophorum vaginatum sol. 57
Carex limosa cop. 7; spar. 14·5; sol. 64·5
Rhynchospora alba cop. 7; spar. 21; sol. 29
Carex rostrata sol. 28·5
C. lasiocarpa sol. 14·5
s. Sphagnum balticum soc. 100
S. recurvum (P.B.) Warnst. sol. 18
S. medium sol. 14
S. dusenii spar. 14

This association (4) far from occurring everywhere only exists in little plots. It also often forms quagmires (Schwingrasen) on peaty lakes surrounded by Sphagnum bog. On the whole the area it occupies is small.

The association (5) *Rhynchospora alba*-Sphagnaceae occurs in little plots in the hollows of the complexes. It also forms but a small share of the bog surface.

B. Ecology of the Species (cf. Fig. 4).

Pinus silvestris is the least exacting tree as regards the content of the soil in mineral salts. It is dominant alike on dry sands and on the moist peat of the Sphagnum bogs, substrata alike poor in mineral salts. *Betula alba* grows chiefly in the Transition bogs which are richer in mineral elements. Ground water at a level of 15 to 20 cm. below the surface is the limit for the presence of *Pinus*, and it only forms an association when the ground water level is lower (30 to 40 cm.). This explains the dominance of *Pinus* only in the drier associations, *P.s.-L.p.-C.c.*-S. and *P.s.-E.v.*-S. It is rare in the wetter associations such as *C.l.*-S., etc. *Ledum palustre* resembles the pine in its relation to moisture, while *Cassandra calyculata* and *Andromeda polifolia* are more hydrophilous.

The height, growth and closeness of stand (see lists in the last section) of the pine diminish with increase of moisture. Thus in *P.s.-L.p.-C.c.*-S. the average height is 5·9 m. (18 plots), in *P.s.-E.v.*-S. it is 4·2 m. (16 plots). In the associations of the hollows the pine does not attain the size of a tree.

Ledum palustre occurs exclusively on the peat poor in salts of the Sphagnum bogs. Like the pine its optimum moisture is found in the driest association, where it is dominant in the undershrub layer, together with *Cassandra calyculata*. In conditions of greater moisture (*P.s.-E.v.*-S.) it occurs only as isolated individuals, and in the wet hollows it disappears entirely. This species is a constant companion of the pine and grows well under its shade.

Cassandra calyculata. Similar to the last in relation to salts. Optimum moisture also like the last, but constantly met with, though not dominant, in the moist associations of the hollows. Like the last it can bear moderate shading.

Andromeda polifolia, like the two last-named species, is characteristic of Sphagnum bog, though rarely dominant. Its optimum moisture tends to be greater than that of *Cassandra*.

The moisture relations of the three last-named species are graphically represented in Fig. 3. Owing to lack of data as to ground water level the four associations are used to indicate the degree of moisture. They show increase of moisture on the horizontal axis, from left to right, and the percentage of frequency for the three species in the different associations is given on the vertical axis.

Eriophorum vaginatum is also a typical species of the Sphagnum bog, though it may be dominant on peat richer in mineral salts where the three species just described are never dominant. It occurs on Transition bogs which have long been drained, and in clearings of birch forest grown on dry bogs, side by side with plants typical of a mineral soil. It also flourishes on burned

peat. On undrained bog its optimum moisture is greater than that of *Cassandra*, but its moisture curve extends further in both directions than those of the three undershrubs, so that it is dominant both in the water-saturated quagmires of turbaries and also on well-drained peat. This considerable amplitude of adaptability as regards both salts and water explains its participation in so many associations. The abundance of winged seeds it produces accounts for its rôle of pioneer on peat destitute of vegetation, whether inundated turbaries or burned peat areas.

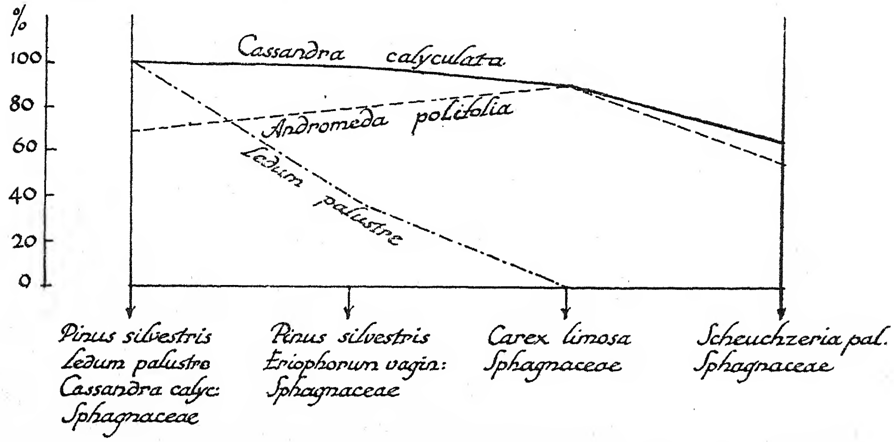

FIG. 3. Graph showing the percentage frequencies of *Cassandra calyculata*, *Andromeda polifolia* and *Ledum palustre* in four associations of the Sphagnum bog.

Scheuchzeria palustris is another typical plant of Sphagnum bog and is confined to the wettest association (*Sch.p.*-Sph.), where the ground water is only a few cm. below the surface.

Rhynchospora alba is again a typical Sphagnum bog species with optimum moisture in *Rh. a.*-Sph., the moisture curve descending abruptly in the direction of the drier associations.

Carex limosa is the third species of the wet bog hollows. Its optimum moisture lies between those of the two previous species and as with them the moisture curve descends abruptly.

Sphagnum medium Limpr. is dominant only in Sphagnum bogs; in Transition bogs it occurs only as isolated individuals. It is the least hydrophilous of the Sphagna dominant in Sphagnum bog, inhabiting the summits of the tussocks. Its optimum moisture lies in the association *P.s.*-*L.p.*-*C.c.*-S., where it can accommodate itself to moderate shade.

Sphagnum recurvum (P.B.) Warnst. is dominant equally in Sphagnum and Transition bogs. In the Sphagnum bogs var. *parvulum* Warnst., together with *S. ambiphyllum* Russ. var. *parvifolium* Sendt, are chiefly found. I believe they are only xerophytic small-leaved ecological forms of *S. recurvum*, which grow in compact masses on the tops of the tussocks with *S. medium*

in the *P.s.-C.c.-L.p.*-Sph. association and predominate in the wetter association *P.s.-E.v.*-Sph. on the sides of the tussocks. This is a species of great adaptability as regards quantity of mineral salts and therefore enters many associations. It can bear more shade than *S. medium*.

Sphagnum balticum Russ. is more hydrophilous than the foregoing and is dominant only in the three wet associations of the hollows, its moisture curve resembling that of the three phanerogamic dominants of these associations.

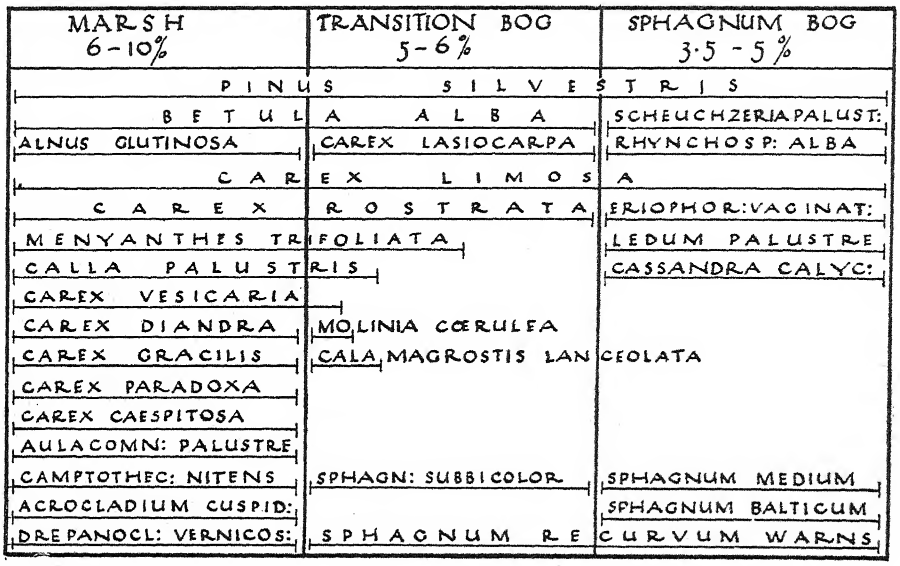

FIG. 4. Amplitudes of adaptability to concentration of mineral salts of species characteristic of Marsh, Transition bog and Sphagnum bog. The percentage figures under these three heads represent, very roughly, the *average percentages of ash* according to Gerassimoff (2), in the peat of the three types. Accurate data on the concentration of salts in the waters are lacking.

Sphagnum Dusenii C. Jensen and ***S. cuspidatum*** Ehrh. are the most hydrophilous of the Sphagnum bog Sphagna. Sometimes they occur in the wettest hollows of the *Sch.p.*-Sph. association with water above the surface.

Hypnum fluitans (Dill) L. This is the species of *Drepanocladus* most adapted to water very poor in mineral salts, and is the sole representative of the genus met with in great quantity in the Sphagnum bogs of Central Russia. Like most of the species of *Drepanocladus* it has floating forms which inhabit the water of inundated turbaries (see below). The terrestrial forms are very common in drying hollows of the Sphagnum bogs.

C. ECOLOGY OF THE ASSOCIATIONS.

Until recently the importance of moisture as a factor in the distribution of the associations of the Sphagnum bog has been insufficiently recognised, though lately, it is true, classifications of bogs according to moisture have

appeared (**16**). The very great difference between the conditions of life on the summits of the tussocks and in the hollows close by (an altitudinal difference of about 70 cm.) corresponds with vegetation of quite different species and must be regarded as mainly due to the difference of moisture (**5**, **6**). The altitudinal zonation from the summits of the tussocks to the bottom of the hollows is represented by the series:

P.s.-L.p.-C.c.-Sph.—	*P.s.-E.v.*-Sph.—	*Rh.a.*-Sph.—	*C.l.*-Sph.—	*Sch.p.*-Sph.
summits of tussocks	slopes	sides of hollows		centres of hollows

This zonation based on moisture may be compared with the series obtained by the use of indicators according to the method of "ecological analysis" described on p. 183. Two groups of indicators are chosen: (1) species whose optimum conditions correspond with the lowest ground water level, and (2) species whose optimum conditions correspond with the greatest excess of moisture. To (1) belong *Pinus silvestris, Betula alba, Picea excelsa, Vaccinium myrtillus, V. vitis-idaea, Ledum palustre, Vaccinium uliginosum*, and certain herbaceous species; to (2) *Scheuchzeria palustris, Rhynchospora alba, Carex limosa*. The average numbers of indicators of the two groups growing in a plot of the four principal associations work out as follows:

	Indicators	
	(1)	(2)
P.s.-L.p.-C.c.-Sph.	3·25	·19
P.s.-E.v.-Sph.	1·78	·33
C.l.-Sph.	·36	2·36
Sch.p.-Sph.	·45	2·43

The indicators of group (1) thus steadily decrease, and those of group (2) increase, in passing from the drier to the wetter associations, corresponding completely with the altitudinal zonation series.

D. SUCCESSION OF ASSOCIATIONS.

Published data (**13**, **14**) on succession in Sphagnum bogs refer only to north-west Russia. Hitherto those of Central Russia have not been studied in respect of succession.

Formation of associations on the periphery of the bogs. The centre of a bog is occupied by an association complex (see p. 183) surrounded by a belt of homogeneous vegetation in which the associations *P.s.-L.p.-C.c.*-Sph. and *P.s.-E.v.*-Sph. predominate. These succeed *Betula alba-Carex lasiocarpa*-Sphagnaceae, and *Pinus silvestris-Carex lasiocarpa*-Sphagnaceae, which are contiguous to them on the edge of the bog (see Fig. 1). The cause of the succession is the overgrowth of the edge of the bog on to the surrounding soil and the consequent giving way of more exacting plants before the advance of less exacting ones. Thus if on the Transition bog *Betula alba* is dominant it will give way before the less exacting *Pinus silvestris*, while if the latter is dominant

it will remain but will be diminished in size and in denseness of stand. Thus in *P.s.-C.l.*-Sph. the mean height of the pines is 6·8 m.: in the Sphagnum bog association *P.s.-L.p.-C.c.*-Sph., 5·9 m., and in *P.s.-E.v.*-Sph., 4·6 m. *Carex lasiocarpa*, the dominant herbaceous plant of the Transition bog, is replaced by *Eriophorum vaginatum* and the undershrubs of the Sphagnum bog, while *Sphagnum recurvum* and *S. subbicolor* partly give way to the less exacting *S. medium*. The microrelief becomes more diversified, probably chiefly because *Sphagnum medium* grows more vigorously than *S. recurvum*, so that the former species forms tussocks round the tree trunks which increase in height above the level of the intervening spaces dominated by the more slowly growing *S. recurvum*. Another cause may co-operate in increasing the differences of level. In years of drought the peat *between* the tussocks shrinks the most because it is fuller of water and less dense, while the denser peat of the tussocks shrinks less because it contains less water and is also consolidated below by the tree roots.

A first indication of the age of an association is its position in relation to the centre of the bog—the nearer to the centre the later the stage of succession. Plant indicators may also be used for the analysis of succession. The indicators chosen should be (1) plants of mineral soils, but occurring also in Sphagnum and Transition bogs (*Pinus silvestris*, *Picea excelsa*, *Betula alba*, *Vaccinium myrtillus*, *V. vitis-idaea*, etc.) and (2) typical Sphagnum bog species (*Ledum palustre*, *Cassandra calyculata*, *Andromeda polifolia*, *Eriophorum vaginatum*, *Drosera rotundifolia*, *D. anglica*, *D. obovata*, *Scheuchzeria palustris*, *Rhynchospora alba*). The application of the method is the same as in the ecological analysis described in Section C. The results were as follows:

		Average numbers of indicators per plot	
		Mineral soil indicators	Sphagnum bog indicators
Associations of Transition bog	*B.a.-C.l.*-Sph.	2·4	1·59
	P.s.-C.l.-Sph.	3·2	2·8
Associations of Sphagnum bog	*P.s.-L.p.-C.c.*-Sph.	1·88	4·38
	P.s.-E.v.-Sph.	1·28	4·05

Thus the two associations of the Sphagnum bog differ from the two of the Transition bog by the smaller number of mineral soil indicators and the larger number of Sphagnum bog indicators. Consequently on a bog in course of formation indicators of the first group decrease and those of the second increase. If the two genetically equivalent associations of the two types are compared this difference does not appear. In each type one of the associations surpasses the other in the number of indicators of *both* groups. This is because there is a greater number of species, owing to the greater dryness, in a plot of *P.s.-C.l.*-Sph. and in a plot of *P.s.-L.p.-C.c.*-Sph. respectively than in a corresponding plot of the other association. These data confirm the results as to relationship of the associations obtained by a study of their situation.

The *Carex limosa*-Sph. association is most often developed from the Transition bog association *Carex rostrata*-Sph. *Carex rostrata* is replaced by the less exacting *C. limosa*, and *Sph. recurvum* yields most of its place to *Sph. balticum.* The whole process takes place in the presence of more moisture than the one described above. The indicator numbers are as follows:

	Mineral soil indicators	Sphagnum bog indicators
Carex rostrata-Sph.	2·40	1·60
C. limosa-Sph.	0·36	3·91

Here again we have the first group of indicators diminishing, the second increasing, confirming the conclusion, derived from its more peripheral position, that the first association is an earlier stage of succession.

Formation of Association-Complexes.

The complexes of Sphagnum bog associations are situated in the central, oldest parts of the large peat bogs (see Fig. 1, p. 179). They occupy no less than half the whole area of the Sphagnum and Transition bogs taken together, and their wide extent demonstrates their durability. Their position, together with the thickness of the peat beneath them, show that they form the final phase of development of the Sphagnum bog vegetation.

The complexes develop from different associations of the peripheral zone, such as *P.s.-L.p.-C.c.*-Sph. and *P.s.-E.v.*-Sph. As soon as *Sphagnum medium* appears on a Transition bog tussocks begin to form and, owing to the rapid growth of this species, attain a considerable size. In the hollows between the tussocks atmospheric water, running down the sides, begins to accumulate, first of all killing the trees in these hollows owing to excess of moisture. Next the undershrubs perish, and the more hydrophilous *Sphagnum balticum* replaces *S. recurvum.* Lastly there appear in the hollows the hydrophilous species *Carex limosa, Rhynchospora alba,* and *Scheuchzeria palustris.*

The development of a complex from the association *Carex limosa*-Sph. occurs as follows. In this association there are always small tussocks because Sphagnum grows very energetically round tufts of *Eriophorum*, undershrubs, etc. When the more xerophilous *Sphagnum medium* appears on these tussocks they grow more rapidly and are finally colonised by *Pinus silvestris* and undershrubs, thus forming a complex with the association of the hollows.

Changes of Association-Complexes.

The associations of a complex are not stable but undergo changes which may bring back an earlier phase of development. These changes have been described in north-west Russia by Soukacheff (**13**) and certain other investigators, in Sweden by Osvald (**11**) in great detail. In Central Russia the process is different to that which obtains in more northern latitudes.

The Sphagnum carpet of the hollows of undrained peat bogs very often begins to die off over areas of thousands of square metres. This is caused by

periods of hot summer drought, which only affect the Sphagna of the hollows, such as *S. balticum*, whose stems then lie horizontally on the peat surface, becoming covered with a crust of algae. The species of the tussocks (*S. medium* and *S. recurvum*) do not suffer from drought though they live in a drier place. Their dense growth enables them to absorb and retain a greater quantity of moisture than the loose growth of *S. balticum*, with its long stems and distant whorls of branches. The whorls of close-set branchlets and the minute leaves of *S. recurvum* form a good water-holding structure, while *S. medium* has a well developed system of pore-bearing hyaline cells. Certainly in Central Russia these tussock Sphagna do not die off owing to drought, nor are they replaced by liverworts and lichens as in more northern latitudes.

In hollows thus deprived of their Sphagnum covering *Hypnum fluitans* (Dill) L., appears as a pioneer, often producing fruit. Sometimes *Rhynchospora alba* appears on the bare peat ("naked *Rhynchospora alba* moor" of Osvald, **11**). The drying up of the hollows favours this species at the expense of its more hydrophilous competitors, *Carex limosa* and *Scheuchzeria palustris*.

If the hollows remain dry, all these associations give place to *Eriophorum vaginatum* on naked peat, which may establish itself at once without the intervention of the pioneers. Tussocks of this species arise from seed coming from the neighbouring hillocks into the hollows, and growing rapidly fill up the hollows with new hillocks. These new tussocks or hillocks become colonised by *Sphagnum medium*, and with the old ones flatten out the microrelief into an approximately level surface (*Eriophorum vaginatum*-Sph. association). In time differentiation of the microrelief begins afresh and the gradual development of a new complex ensues. If the drying of the hollows is only temporary, *Eriophorum vaginatum* does not establish itself and *Carex limosa*-Sph. association re-develops.

3. TRANSITION BOG (UEBERGANGSMOOR)

A. Associations.

1. Association *Betula alba-Molinia caerulea*-Sphagnaceae.

md.	Betula alba cop.		Equisetum silvaticum sol.
ma.	Pinus silvestris sol.	*g.*	Molinia caerulea cop.
	Picea excelsa sol.		Calamagrostis lanceolata sol.
p.	Rhamnus frangula sol.		Carex vesicaria sol.
n.	Vaccinium vitis-idaea sol.	*b.*	Polytrichum commune sol.
	V. myrtillus sol.		Hypnum Schreberi sol.
h.	Menyanthes trifoliata sol.	*s.*	Sphagnum recurvum Warnst. cop.
	Calla palustris sol.		S. Girgensohnii sol.
	Trientalis europaea sol.		S. subbicolor sol.

This association is found in little plots, rarely more than 10 m. square, on the very limit of the Transition bog and the forest on mineral soil. On the whole this association covers an insignificant part of the surface belonging to the Transition bog. Frequently it forms also a narrow ring round the peat lakes, surrounded by Sphagnum bogs.

2. Association *Betula alba-Carex vesicaria*-Sphagnaceae.

md. Betula alba cop.
ma. Pinus silvestris sol.
Picea excelsa sol.
p. Rhamnus frangula sol.
h. Menyanthes trifoliata sol.
Comarum palustre sol.
Peucedanum palustre sol.
Naumburgia thyrsiflora sol.
Calla palustris sol.
Lysimachia vulgaris sol.
Equisetum silvaticum sol.
g. Carex vesicaria cop.
Calamagrostis lanceolata sol.
Carex lasiocarpa sol.
s. Sphagnum recurvum Warnst. soc.

Like the preceding association, this is met with in little plots on the extreme limit of the Transition bog with mineral soil. The surface it occupies is very small.

3. Association *Betula alba-Calla palustris*-Sphagnaceae.

md. Betula alba spar.
ma. Pinus silvestris sol.
Picea excelsa sol.
n. Cassandra calyculata sol.
h. Calla palustris soc.
Menyanthes trifoliata sol.
s. Sphagnum recurvum Warnst. spar.

This association occurs in plots of larger size than the preceding ones, not seldom attaining 100 square m. It also establishes itself in the peripheral belt of the Transition bog, not far from the mineral soil. On the whole it likewise takes up small spaces on the Transition bogs.

4. Association *Betula alba-Menyanthes trifoliata*-Sphagnaceae.

md. Betula alba spar.
ma. Picea excelsa sol.
n. Salix repens sol.
S. lapponum sol.
Betula humilis sol.
Vaccinium oxycoccus sol.
Cassandra calyculata sol.
Andromeda polifolia sol.
h. Menyanthes trifoliata cop.
Naumburgia thyrsiflora sol.
Peucedanum palustre sol.
Comarum palustre sol.
Equisetum heleocharis sol.
Galium palustre sol.
Caltha palustris sol.
Carex lasiocarpa sol.
Calamagrostis lanceolata sol.
Molinia caerulea sol.
Carex stricta sol.
C. vesicaria sol.
C. rostrata sol.
b. Hypnum schreberi sol.
Hylocomium splendens sol.
s. Sphagnum recurvum cop.

This association is found in plots of a considerable size, sometimes of several hundreds of square metres, and is of greater importance for the general aspect of the Transition bogs than any of the three preceding ones. But all four together occupy a very insignificant area compared with the two which follow.

5. Association *Betula alba-Calamagrostis lanceolata*-Sphagnaceae.
(Compound list from seven separate plots.)

md. Betula alba soc. 14; cop. 71·5; spar. 14·5
Populus tremula sol. 14
ma. Pinus silvestris sol. 57
Picea excelsa sol. 57
Salix aurita spar. 14; sol. 57
Rhamnus frangula sol. 28·5
Viburnum opulus sol. 14
Salix cinerea sol. 14
Rubus idaeus sol. 14
n. Cassandra calyculata sol. 14
Vaccinium oxycoccus sol. 14
V. myrtillus sol. 43
V. vitis-idaea sol. 28·5
h. Comarum palustre spar. 14·3; cop. 14·3; sol. 57
Naumburgia thyrsiflora sol. 71·5
Menyanthes trifoliata sol. 57

Peucedanum palustre sol. 43
Galium palustre sol. 43
Ranunculus lingua sol. 28·5
Equisetum silvaticum sol. 28·5
Melampyrum nemorosum sol. 28·5
Trientalis europaea sol. 28·5
Epilobium angustifolium sol. 14
Pirola rotundifolia sol. 14
Potentilla silvestris sol. 14
Epilobium palustre sol. 14
g. Calamagrostis lanceolata cop. 86; spar. 14
Carex lasiocarpa cop. 14; spar. 14; sol. 29
Phragmites communis spar. 43; sol. 14
Carex canescens sol. 43
Agrostis canina spar. 14; sol. 15
Deschampsia caespitosa sol. 29
Carex vulgaris sol. 29
Juncus effusus sol. 14
Molinia caerulea sol. 14
Carex vesicaria sol. 14
C. rostrata sol. 14
b. Polytrichum commune sol. 28·5
Hypnum schreberi sol. 28·5
Dicranum undulatum sol. 14
Aulacomnium palustre sol. 14
Climacium dendroides sol. 14
Hylocomium splendens sol. 14
s. Sphagnum recurvum soc. 43; spar. 28·5; sol. 28·5
S. squarrosum sol. 28·5

This association occurs in plots of greater extension than any of the preceding and on the whole takes up large areas. It exists almost invariably on Sphagnum peat bogs with active peripheral growth and surrounded by forest. Here it forms a band of a few metres in width on the limit of the mineral soil.

6. Association *Betula alba-Carex lasiocarpa*-Sphagnaceae.
(Compound list from seventeen plots.)

md. Betula alba cop. 6; spar. 30; sol. 35
Populus tremula sol. 12
ma. Pinus silvestris sol. 53
Picea excelsa sol. 18
p. Salix aurita spar. 6; sol. 35
S. repens sol. 35
S. lapponum sol. 35
S. myrtilloides sol. 23·5
S. cinerea sol. 12
Rhamnus frangula sol. 12
Salix pentandra sol. 6
n. Cassandra calyculata sol. 82·5
Vaccinium oxycoccus spar. 6; sol. 70·5
Andromeda polifolia sol. 35
Ledum palustre sol. 12
Vaccinium vitis-idaea sol. 12
V. myrtillus sol. 12
h. Comarum palustre spar. 18; sol. 53
Menyanthes trifoliata spar. 6; sol. 65
Naumburgia thyrsiflora sol. 53
Peucedanum palustre sol. 47
Equisetum heleocharis spar. 52; sol. 35
Epilobium angustifolium sol. 18
E. palustre sol. 12
Galium palustre sol. 30
Orchis maculata sol. 12
Drosera rotundifolia sol. 12
Calla palustris sol. 6
Scutellaria galericulata sol. 6
Viola epipsila sol. 6
Lysimachia vulgaris sol. 6
g. Carex lasiocarpa soc. 36; cop. 53; spar. 11
Calamagrostis lanceolata cop. 6; spar. 12; sol. 41
Carex rostrata sol. 41
C. limosa sol. 41
C. chordorrhiza sol. 23·5
C. canescens sol. 18
Eriophorum vaginatum sol. 18
E. angustifolium sol. 6
Molinia caerulea sol. 6.
Deschampsia caespitosa sol. 6
Carex vesicaria sol. 6
Agrostis canina sol. 6
Phragmites communis sol. 6
b. Polytrichum commune sol. 47
Hypnum schreberi sol. 18
Dicranum bonjeani sol. 6
s. Sphagnum recurvum Warnst. soc. 76; cop. 6; spar. 12; sol. 6
S. medium sol. 18
S. subbicolor sol. 12
S. squarrosum sol. 6

This association occupies a greater surface on Transition bogs than all the other associations taken together. It extends uninterruptedly over considerable areas, not seldom thousands of square metres.

7. Association *Pinus silvestris-Carex lasiocarpa*-Sphagnaceae.
(Compound list from five plots.)

md. Betula alba cop. 20; sol. 40
Populus tremula sol. 20
ma. Pinus silvestris cop. 60; spar. 20; sol. 20
Picea excelsa sol. 20
p. Salix aurita spar. 40
n. Vaccinium oxycoccus cop. 20; sol. 60
Cassandra calyculata spar. 20; sol. 60
Ledum palustre sol. 60
Andromeda polifolia sol. 40
Vaccinium myrtillus sol. 40
V. uliginosum sol. 20
h. Orchis maculata sol. 20
g. Carex lasiocarpa cop. 90; spar. 10
Calamagrostis lanceolata cop. 20; spar. 20
Eriophorum vaginatum cop. 20; spar. 20; sol. 60
Molinia caerulea sol. 20
b. Polytrichum strictum sol. 60
Hypnum schreberi sol. 40
s. Sphagnum recurvum soc. 40; cop. 60
S. subbicolor soc. 20; cop. 40
S. medium sol. 20
l. Cladonia rangiferina sol. 20

This association covers considerable spaces on Transition bogs, only surpassed in this respect by the preceding one. It is found in plots of hundreds and thousands of square metres.

8. Association *Carex rostrata*-Sphagnaceae.
(Compound list from five plots.)

md. Betula alba sol. 100
ma. Pinus silvestris sol. 80
Picea excelsa sol. 40
p. Salix aurita sol. 20
h. Menyanthes trifoliata spar 20; sol. 80
Naumburgia thyrsiflora sol. 40
Comarum palustre sol. 40
Epilobium palustre sol. 20
Equisetum heleocharis sol. 20
Calla palustris sol. 20
Galium palustre sol. 20
Utricularia vulgaris sol. 20
Alisma plantago sol. 20
Ranunculus lingua sol. 20
g. Carex rostrata soc. 20; cop. 60; spar. 20
C. lasiocarpa sol. 60
Calamagrostis lanceolata sol. 40
Carex vesicaria sol. 40
Eriophorum vaginatum sol. 40
Carex vulgaris sol. 20
C. canescens sol. 20
C. limosa sol. 20
Scheuchzeria palustris spar. 20
n. Cassandra calyculata sol. 40
Andromeda polifolia sol. 40
Vaccinium oxycoccus sol. 40
Ledum palustre sol. 20
Vaccinium vitis-idaea sol. 20
b. Hypnum schreberi
Polytrichum commune
Aulacomnium palustre
Dicranum bonjeani
s. Sphagnum recurvum soc. 40; cop. 40; spar. 20
S. medium sol. 40
S. squarrosum sol. 40
S. obtusum sol. 20

This association often covers hundreds of square metres of treeless Transition bog on mineral soil at the edge of meadow associations, and is the most extensive of treeless Transition bog associations.

The *Menyanthes trifoliata*-Sphagnaceae association (not described here) is the only remaining Transition bog association that plays any considerable part in the general aspect of the vegetation covering.

B. Ecology of the Species. (Cf. Fig. 4, p. 188.)

The formation of new peat in the Transition bog exceeds its decomposition and therefore the bog continually grows in height. As this happens the roots of the plants are removed further from the ground water table and are increasingly fed with atmospheric water so that the concentration of mineral

salts in the water feeding the plant roots becomes less and less. The different species show different powers of adapting themselves to this change.

Carex vesicaria grows in company with *C. gracilis* on marshes, and occurs also on Transition bogs which are just forming on mineral soil (cf. Fig. 4). It is dominant mainly in places where water stands in spring, but which are comparatively dry in summer. It is more hydrophilous than *C. gracilis*, so that it occupies lower levels in the microrelief. It stands shading fairly well.

Molinia caerulea occurs as isolated plants on marshes, and, like *Carex vesicaria*, than which it is rather more xerophilous, it forms associations on very recent Transition bogs. It also bears shading fairly well.

Calla palustris has a greater range of adaptation to varying concentration of mineral salts than the two preceding species, so that although it occurs on marshes it also forms an association on older Transition bogs. It is more hydrophilous than *Carex vesicaria* and bears shading well.

Menyanthes trifoliata has an even greater range of adaptability to differences in concentration of mineral salts, so that it is dominant in a number of associations from marshes to older Transition bogs. It also has a great range in respect of adaptation to water. It tolerates shading fairly well.

Calamagrostis lanceolata is dominant only on Transition bogs of the same age as those where *Calla palustris* flourishes. Its relation to water is intermediate between those of *Molinia* and *Calla*. It bears shading fairly well.

Carex lasiocarpa is a typical plant of the Transition bog, very well adapted to the varying conditions of existence on the growing surface of the peat, and can tolerate a lower concentration of mineral salts than any of the preceding species, so that it occurs on older bogs. Rarely (as on the Tatischevo marshes) it is dominant where the hardness of the water rises to 20 (German) degrees. It is more hydrophilous than the preceding species and can bear moderate shading.

Carex rostrata ranges from water of 25 degrees of hardness to bogs slightly younger than those in which *C. lasiocarpa* flourishes. It is more hydrophilous than that species and likes slowly flowing water. It does not tolerate shading.

C. Ecology of the Associations.

The associations of the Transition bog are not genetically equivalent, but form a developmental series beginning with boggy forests and ending with the Sphagnum bogs. It is moisture which determines the distribution in space of the associations which are more or less genetically equivalent. The following lists of associations are in order of increasing moisture:

Younger associations	Older associations
Betula alba-Molinia caerulea-Sphagnaceae	*Betula alba-Calamagrostis lanceolata*-Sphagnaceae
Betula alba-Carex vesicaria-Sphagnaceae	*Pinus silvestris-Carex lasiocarpa*-Sphagnaceae
{ *Betula alba-Calla palustris*-Sphagnaceae	*Betula alba-Carex lasiocarpa*-Sphagnaceae
{ *Betula alba-Menyanthes trifoliata*-Sphagnaceae }	*Carex rostrata*-Sphagnaceae

Using as indicators species of mineral soil which require little water we obtain a series corresponding completely with the moisture series above. With increase of moisture the number of mineral soil indicators decreases.

Betula alba-Calamagrostis lanceolata-Sph.	5·0	*Betula alba-Carex lasiocarpa*-Sph.	2·41
Pinus silvestris-Carex lasiocarpa-Sph.	3·2	*Carex rostrata*-Sph.	2·40

The small difference between the last two figures is due to the small number of plots of the last association investigated. The number of plots of the younger associations given in the moisture series above was insufficient for the application of this method of analysis.

D. SUCCESSION OF ASSOCIATIONS.

The associations of the Transition bog are in a state of unstable equilibrium. They form a continuous developmental series, beginning with the associations of the mineral forest or meadow soil and ending with the Sphagnum bog complex. Under existing climatic conditions this process of development, when once it begins, tends to continue to its natural climax, each association making its own continued existence impossible, and furnishing the conditions for the formation of a succeeding one.

There is no doubt that this gradual transformation of forest into bog also took place in former times, and that on a large scale. The layer of Sphagnum-sedge peat with abundant pine wood occurring at the bottom of most of the bogs is evidence that they were formed chiefly by the gradual invasion of coniferous forest by the bog plants. The processes of succession involved, the longest and most complicated of which is the transformation of spruce-birch forest into bog, have not yet been described in any detail for Central Russia. The chief criterion of the position of an association in the genetic series is its relation to the centre of the bog. The nearer it is to the centre the later it stands in the genetic series. Measurement of the thickness of the peat affords indirect confirmation of conclusions reached in this way. The extent of surface occupied is a measure of the relative duration of an association—the greater the area the more long-lived is an association on the whole. The means of propagation of the species must also be considered.

The typical forest association is *Picea excelsa-Vaccinium myrtillus-Hypnum schreberi* with abundance of *V. vitis-idaea*. The transformation usually begins with the appearance of *Polytrichum commune*. Its dense tufts spread rapidly and stifle the other mosses and the flowering plants. A zone of *Picea excelsa-Polytrichum commune*, a few metres wide, commonly occurs in spruce forests which are beginning to be transformed into bog. *Polytrichum commune* retains moisture in its dense tufts and makes possible the establishment of the more hydrophilous *Sphagnum girgensohni*. The *Picea excelsa-Polytrichum commune* association gives way to the association *Picea excelsa-Sphagnum girgensohni*. Neither of these associations is long-lived. The appearance of *Sphagnum recurvum* P.B. and the beginning of peat formation is accompanied by the

rapid dying off of the spruce, which does not regenerate. *Betula alba* becomes predominant, *Sphagnum recurvum* forms the moss-carpet, and the forest species give way to bog species. This marks the establishment of Transition bog proper.

The associations of the Transition bog are disposed in concentric circles round the centre of the bog (Fig. 1). On the very edge of the mineral soil small islets of *Betula alba-Carex vesicaria*-Sph. and *Betula alba-Molinia caerulea*-Sph. are scattered. The shallowness of the peat, which does not exceed a few centimetres, and the smallness of the areas of these associations, point to their short duration.

Further towards the centre of the bog extend the associations *Betula alba-Calla palustris*-Sph. and *Betula alba-Calamagrostis lanceolata*-Sph. There may be from 15 to 40 cm. of peat under the last-named (Masslovo Bog, District of Bogorodsk, Gov. of Moscow), and this shows that the bog has already passed through decades or even centuries of development, while the considerable size of the areas indicates comparative stability. This association in fact extends almost everywhere along the wooded borders of the bogs.

Next comes the association *Betula alba-Menyanthes trifoliata*-Sph. on still thicker peat, and then a wide belt of *Betula alba-Carex lasiocarpa*-Sph. on peat up to 100 cm. and more in depth, extending over hundreds or thousands of square metres, indicating its relative longevity. This association in fact occupies more space than all the earlier ones (which tend to occur as islands in it) put together, so that we may conclude that its longevity is also greater than that of all the others together. In regard to the fate of *B.a.-C.l.*-Sph., see p. 189.

Individual associations may of course be missing from any given successional series.

Analysis by means of indicators confirms the conclusions drawn from the position of the associations.

	Mineral soil indicators	Sphagnum bog indicators
Betula alba-Calamagrostis lanceolata-Sph.	5·29	1·86
Betula alba-Carex lasiocarpa-Sph.	2·41	3·94

Not enough plots of the genetically earlier associations were examined to enable an indicator analysis to be made.

The succession from pine forest to Sphagnum bog passes through a smaller number of stages than the succession from spruce forest (see Fig. 1). This is because the sandy soil on which the pine forest grows is poorer in mineral salts, so that the last stage can be reached more rapidly. Very often the development begins with the development of a sphagnum carpet with *Carex lasiocarpa* in the pine forest itself (*P.s.-C.l.*-Sph.). Then comes *Pinus silvestris-Ledum palustre-Cassandra calyculata*-Sph. or *Pinus silvestris-Eriophorum vaginatum*-Sph. (Fig. 1). Sometimes the succession is still shorter, the pine forest passing directly into a bog, oftenest into *P.s.-L.p.-C.c.*-Sph. (The Birch-*Calamagrostis*-Sph. stage does not occur.)

When treeless meadow develops into bog the association *Carex rostrata*-Sph. appears. This cannot be dealt with here.

4. INFLUENCE OF CULTURE ON THE VEGETATION OF SPHAGNUM AND TRANSITION BOGS

DRAINAGE.

If the drainage is very complete the bog vegetation disappears altogether and the peat becomes inhabited by a varied ruderal flora (*Rumex acetosella*, *Epilobium angustifolium*, etc.). With moderate drainage the bog plants survive but different species show varying degrees of resistance. *Vaccinium uliginosum* is more resistant than most, so that in moderately drained *P.s.-L.p.-C.c.*-Sph.

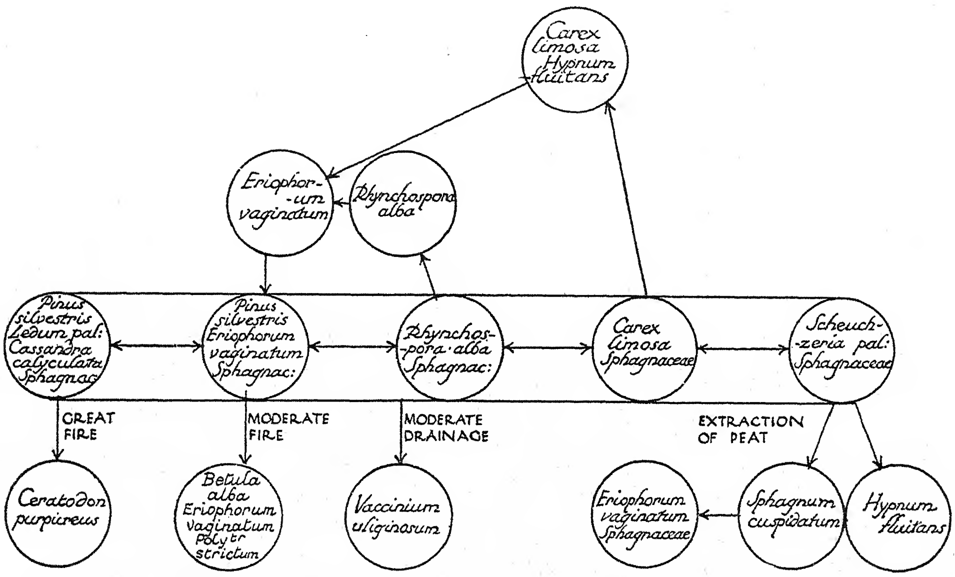

FIG. 5. Transformations of associations of the Sphagnum bog in nature and as a result of artificial interference.

The central horizontal row of five circles represents the changes of the associations of the central bog complex, which may proceed in either direction, from more xerophytic (left) to more hydrophytic (right) or vice versa (see p. 192). The upper circles represent the associations which are formed after the dying off of Sphagna in the hollows, bringing about the levelling of the uneven microrelief. The lowest horizontal row represents the changes in vegetation brought about by fires, drainage and peat extraction.

it often predominates (Fig. 5), though playing an altogether subordinate part in the untouched association. I have observed thousands of square metres of luxuriant *V. uliginosum* during the first stages of draining, and even on completely drained bogs where peat is being dug the species occurs in large groups.

Eriophorum vaginatum does not bear drainage so well, though it occurs almost pure along the sides of sufficiently damp turbaries. When the plants are in fruit such places can be picked out from a distance by their dazzling

white colour. The hydrophilous *Carex limosa*, *Rhynchospora alba* and *Scheuchzeria palustris* disappear first on drainage; also the Sphagna, *S. medium* holding out longer than *S. recurvum*.

EXTRACTION OF PEAT (see Fig. 5).

The vegetation of turbaries depends on (1) the type of bog, (2) the thickness of the untouched peat, (3) the depth of water in the turbary, (4) the age of the turbary.

The colonisation of Sphagnum bog turbaries which are constantly inundated proceeds as follows. The pioneers are the floating Sphagna (most often *S. cuspidatum*) or the genus or subgenus Drepanocladus (Harpidium), most often *Hypnum* (*Drepanocladus*) *fluitans*. At first the separate moss plants grow horizontally, but gradually, as they multiply and exercise lateral pressure upon one another, they become vertical and the dense mass forms a platform on which *Eriophorum vaginatum* can establish itself. This species colonises easily by its flying seeds always ripening in abundance, and is scattered from the peat heaps left by the extracting engines. On turbaries thirty years old the tufts of *Eriophorum* are usually in lateral contact, but with their bases separated by a quagmire covered by Sphagnum which hides the surface of the water (Fig. 5). *Carex limosa* is absent from this habitat which seems most suitable for it. The explanation is that this species disappears from the bog as soon as drainage begins and its seeds are too heavy to travel any distance.

On the turbaries which are not inundated forest of *Betula alba* develops with a ground vegetation of various marsh-loving species.

The colonising vegetation depends also on the proportion of mineral salts in the water and on its reaction. Poverty in mineral salts and an acid reaction are favourable to the development of Sphagnum bog plants. The inundated turbaries of Transition bogs, especially those with a mineral bottom, are colonised by aquatic plants, most often *Hydrocharis morsus-ranae*, *Lemna trisulca*, *Nymphaea candida*, more rarely *Stratiotes aloides*. If the water is not too deep there appears, after the aquatic species or sometimes with them, an association of *Equisetum heleocharis*. The stems of this plant form a dense growth above water, while its rhizomes, intertwining below, give the bog plants a substratum on which they can fix themselves. Very often the colonisation by *Equisetum* is accompanied by the spreading of a moss carpet over the surface of the water, most often formed by *Hypnum aduncum* Hedw.[1] and *Sphagnum teres* Ångstr. Thus we have the two associations: *Equisetum heleocharis*-Sph. (Bystroe marsh, district of Bogorodsk, Gov. of Moscow) and *Equisetum heleocharis*-Hypnaceae (turbaries near Bisserov, district of Bogorodsk). In deeper and more peaty basins *Typha latifolia* takes the place of *Equisetum heleocharis*.

The ultimate fate of these aquatic associations is passage into the typical

[1] Kindly determined by Dr H. Paul, of Munich.

associations of the Transition bog, *Carex rostrata*-Sph. and *Carex lasiocarpa*-Sph. In the Bystroe marsh, where a little river has been absorbed by the bog, a picture of the succession of *Equisetum heleocharis* to *Carex lasiocarpa* can be observed. At the same time the floating Sphagnum covering thickens. In the middle of the former river-bed there is a dark green belt of *Equisetum heleocharis* growing on a carpet of *Sphagnum teres*. Nearer the banks the vegetation is lighter green due to *Carex lasiocarpa* and the carpet of Sphagnaceae is denser. One can easily walk across the bog on the floating Sphagnum carpet: only here and there are spaces of open water covered by aquatic plants and surrounded by *Equisetum heleocharis*. The succession is:

$$\left.\begin{array}{l}\text{Nuphar luteum} \rightarrow \\ \text{Potamogaton natans} \rightarrow\end{array}\right\} \text{Equisetum heleocharis} \rightarrow \left\{\begin{array}{c}\text{Equisetum heleocharis-}\\ \text{Sphagnum}\end{array}\right\} \rightarrow \left\{\begin{array}{c}\text{Carex lasiocarpa-}\\ \text{Sphagnum}\end{array}\right.$$

In the turbaries near the village of Bisserovo the succession is as follows:

$$\begin{array}{l}\text{Hydrocharis morsus-ranae} \rightarrow \\ \text{Nymphaea candida} \rightarrow\end{array} \left\{\begin{array}{l}\text{Equisetum heleo-} \\ \quad\text{charis} \rightarrow\end{array}\right. \left\{\begin{array}{c}\text{Equisetum heleocharis-}\\ \text{Hypnaceae}\end{array}\right\} \rightarrow \left\{\begin{array}{c}\text{Carex rostrata-}\\ \text{Hypnaceae}\end{array}\right.$$

The colonisation of the deeper turbaries of the Transition bogs with a layer of peat at the bottom, is simpler. The large quantity of salts in the water evidently prevents the development of aquatic plants and of *Equisetum heleocharis*, which is also hindered by the great depth of the water. Turbaries of this type are generally colonised from the sides by floating Sphagna, upon which grows *Carex rostrata*, and this *C.r.*-Sph. association covers hundreds of square metres, its development being made possible by the chemical content of the water.

EFFECT OF FIRES (see Fig. 5).

Fires are very common on Sphagnum bogs. Their effect depends upon their intensity. A great fire destroys all the vegetation and may even level the surface of a hillocky peat bog. The burn is invaded by various plants from other habitats, very often by mosses, principally *Ceratodon purpureus* (Fig. 5). The primordial vegetation re-establishes itself only very gradually.

A moderate fire dries up the surface of the bog to a certain extent and reduces the top layer of peat to ashes. Since the peat is thus enriched by mineral salts the more exacting *Betula alba* takes the place of *Pinus silvestris*. In the herbaceous layer *Eriophorum vaginatum* develops luxuriantly. The Sphagna are replaced by *Polytrichum strictum* Banks, which is constantly seen on the tussocks of the Sphagnum bog, and after a fire develops in immense quantity and fruits abundantly. The mass of its capsules on a stretch of burnt bog can be seen from a distance by their red-brown colour. This association, *B.a.-E.v.-Pol.str.*, is widely spread on burns. *Eriophorum vaginatum* in great quantity is also seen on the burns of Transition bogs.

Fires have a great influence on the life and development of the whole bog. Borders of bogs near villages are in general subject to continual fires. The

covering of Sphagnum almost totally disappears, the development of the bog ceases, and *Eriophorum vaginatum* and *Polytrichum strictum* permanently establish themselves.

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STUDIES ON THE ECOLOGY OF ENGLISH HEATHS

II. EARLY STAGES IN THE RECOLONISATION OF FELLED PINEWOOD AT OXSHOTT HEATH AND ESHER COMMON, SURREY

By V. S. SUMMERHAYES and P. H. WILLIAMS.

(*With Plates II, III and ten Figures in the Text.*)

CONTENTS.

INTRODUCTION

As mentioned in Part I (**11**), during the late war (November 1916–October 1917) a considerable portion of the older part of the pinewood at Oxshott Heath and Esher Common was felled. Since then recolonisation has been proceeding actively making it in many respects the most interesting part of the Common. Our first visit being in October 1920, the account is in some ways incomplete, but we have been enabled to add to it by the kindness of people who had visited the Common in the interim. In addition the extensive fires in 1921 rendered nugatory much of the colonisation prior to that date; thus the process was delayed and we were able, so to speak, to gain time. Although the succession on the felled area has reached only a comparatively early stage, yet we feel that the position is of sufficient interest and affords enough material to justify description now. It was hoped to follow the progress of recolonisation and to publish further accounts at such future times as might seem proper, but unfortunately the authorities have now decided to replant the area at an early date so that it will not be possible to complete our observations. Indeed a small area was planted with pines during the spring of 1925, but the interference with the natural course of events has not yet been very considerable. In spite of this sudden termination to the work it still seems of value to publish the observations, etc., already made, and we hope that we may be able to follow the later phases elsewhere.

Much of the earlier work embodied in this account was done in conjunction with the late Mr L. W. Cole whose many helpful suggestions and indefatigable industry have contributed greatly to the completion of the work. Mr Paul Richards has been studying the Bryophytes and Lichens of the commons during the past two years, and has kindly supplied us with much information with respect to the ecology of these groups. We should also like to express our thanks to Messrs Somerville Hastings, W. J. Lucas and R. Paulson for information about the condition of the Common prior to felling and from that time until 1920; to Mr R. E. Hunter for help in some of the surveying; and to the British Rainfall Organisation for the rainfall data given.

An examination of the map in Part I (**11**, p. 289) will show that the felled area occupies the northern half of the Common, including the whole of the North Ridge and the northern and central valleys. It forms a continuous stretch with the exception of the large isolated circular felled region ("Inner Circle") just north of Sandy Lane which is separated from the main felled area by a narrow strip of pines. To the east, just north of Copsen Farm, the felled region adjoins the original heathland of Round Hill and vicinity; elsewhere it is bordered by woodland or wooded parkland.

The pinewood in the felled part was considerably older (60–90 years of age) at the time of felling than the part now standing, this being probably the explanation of the partial felling. The felling was somewhat irregular, as

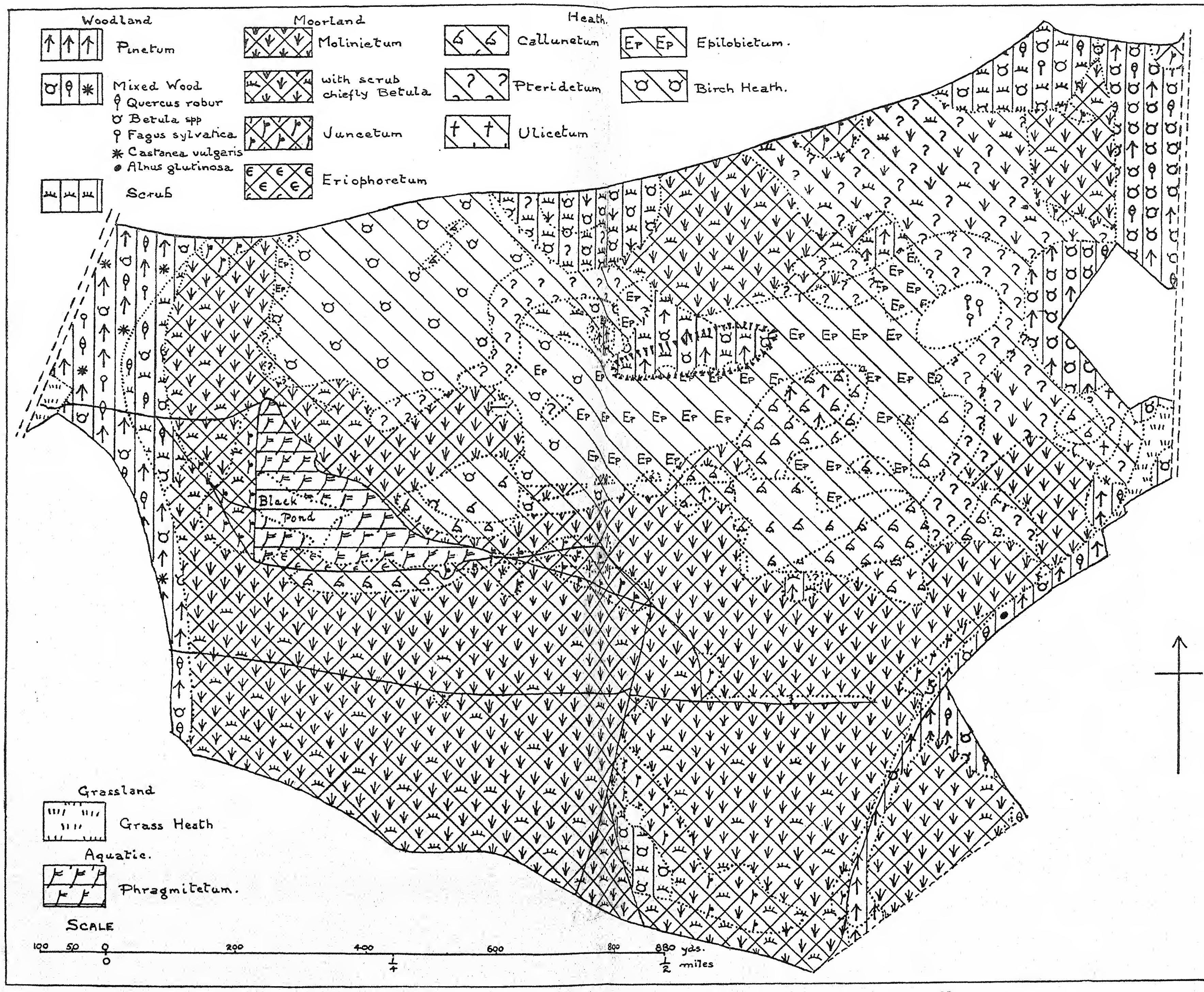

FIG. 1. Vegetation map of Esher Common and northern part of Oxshott Heath from survey carried out in 1921.

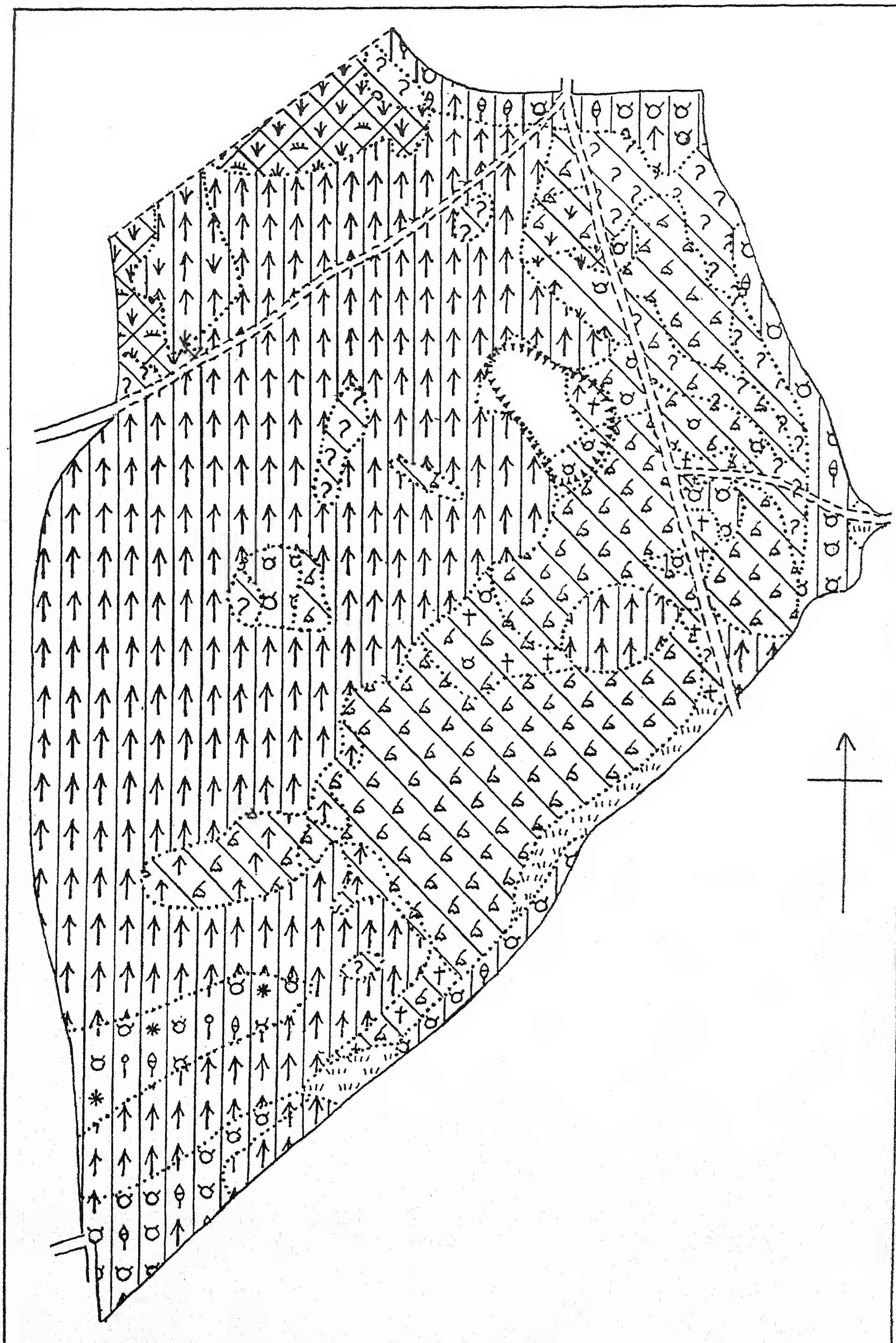

Fig. 2. Vegetation map of southern part of Oxshott Heath. Scale and symbols as in Fig. 1.

can be seen from the map (see Part I), for while the older trees were generally completely removed yet clumps of trees, marginal strips and isolated specimens were left in places. The conditions in the pinewood before felling are unfortunately unknown to us personally, but from verbal accounts the wood generally resembled the part still standing. The higher parts had no ground vegetation at all in most places. On much of the damper ground stunted tufts of *Molinia* had survived since the pine colonisation some 60 to 70 years previously. There were bog areas along the valley crossing the "neck" north of Sandy Lane, just north of the Great Plantation and around Black Pond, there being a well-developed Juncetum at the eastern end of the latter. The most striking change since felling has been the great extension of the wet-type communities. It was the conversion of a dry woodland into bog communities subsequent to felling that first drew our attention to the region.

A detailed survey of the vegetation of the Common was made on a scale of 12 ins. to 1 mile in the early part of 1921 and the results are given on the accompanying maps (Figs. 1 and 2). On the map the outlines of all the principal communities are traced and the state of colonisation of the felled areas at that time can be easily seen.

The mode of representation of the vegetation follows in all but a few details the scheme outlined by Salisbury in this JOURNAL, **8**, No. 1, 1920, pp. 60–61. This scheme has been found quite satisfactory, the basis and species symbols being employed with certain modifications. Two new species symbols have been introduced for *Castanea sativa* and *Epilobium angustifolium* respectively. The area to be mapped here, however, is in a state of rapid succession so that it was necessary to introduce a few new types of representation. Such for instance is the method of representing the invasion of a Molinietum by birch scrub: another example is the variable spacing of the species symbols to denote different degrees of openness in the plant covering. The point at which a moorland community with scrub is converted cartographically into scrub with the woodland basis symbol is naturally arbitrary but corresponds roughly with a continuous scrub 6 ft. in height. "Birch Heath" is used on this map to denote heathy parts with young birches dominant or co-dominant and not for places where the birches are full-grown, which are included in "Mixed Wood" (see Part I). It was decided also to put in "Grass Heath" under the grassland basis symbol rather than class it as a type of heath.

It may also be mentioned that the distances between the basis symbol lines were originally just over 0·2 inch (5 mm.), this being found convenient since it gives ample room in which to draw the species symbols.

1. COMMUNITIES ARISING AFTER FELLING

The communities resulting from recolonisation can be divided into two series, viz. Dry Series and Damp Series. These two are not always clearly separable, there being quite wide transitional zones in places in which the

dominants of the two series are in competition, and which in other respects show special features.

A. Dry Series.

These are communities developing on the higher and drier parts of the felled areas where water does not lie at all during the winter. From Fig. 1 it can be seen that the dry areas form a continuous zone across the centre of the felled region. On felling a large region almost bare of vegetation was produced and on this area, owing to its exposed position, especially along the North Ridge, the surface soil rapidly dried out. On the crest itself the wind soon removed the needle covering, but on the lower slopes this was retained and exerted a very important influence on the developing vegetation. This acid litter and peat is very unfavourable for plant life as the surface dries out almost completely in dry weather, with the result that colonisation was very slow until the surface layer became decomposed more completely. At this point, however, another adverse factor came into play, namely, the formation of "surface scale." Farrow (**4**, p. 149) has noticed the unfavourable effect of surface scale on colonisation. At Oxshott a thin layer (half an inch = 1·25 cm.) of semi-decomposed pine litter tends to dry up and shear away from the soil beneath in dry weather, particularly around pine stumps. Any seeds falling on this area and germinating after rain would find themselves cut off from below with a considerable crack to traverse and would die of drought if dry weather supervened. It was observed in 1923 that more *Calluna* seedlings appeared where no "scale" existed or where the surface was almost pure sand. Where seedlings were found in "scale" areas they were almost invariably associated with the vertical cracks in the surface layer. That the actual nature of the peat at this stage was not inhibitive *per se* was shown by the fact that in places many *Calluna* seedlings occurred where the surface was pure powdery peat. As a result of these various factors colonisation was postponed in many places until the peat layer was almost completely denuded. The delaying effect of the undecomposed humus-layer is still well shown on some of the lower ridges where a combination of good drainage and comparative protection from wind has prevented the rapid removal of the peat.

(I) *The Pioneer Phase.*

A number of pioneer communities have been developing on the dry areas since the felling, most of them being dominated by a single species. The following plants have formed such communities in varying degrees: *Pteridium aquilinum*, *Calluna vulgaris*, *Epilobium angustifolium* and *Betula* spp. (*B. alba* and *B. pubescens*). These species did not all start equal in the competition for the new ground: *Pteridium* was already present as communities in the pinewood, *Calluna* occurred as isolated individuals in the body of the wood or as larger patches in openings, while both *Betula* and *Epilobium* have had

to migrate from outside. These differences have played a large part in determining the course of recolonisation.

After felling the first development of the plants in the drier regions was the recovery of *Pteridium* and isolated Ericaceous shrubs. The degree to which the latter had survived in the older pinewood is not known, but in view of the greater age of this part of the wood compared with the existing part it seems likely that they had done so in very favourable spots only. There are however several places where the pines had apparently never reached any great size, and there heath vegetation persisted.

(a) *PTERIDIUM AQUILINUM* CONSOCIES.

Pteridium, which spreads by rhizome growth only in these dry regions, forms communities very similar to those described in Part I. The districts covered by *Pteridium* at present are in all probability the same as those occupied in the original wood, although increase in area has taken place. As far as we are aware, no new *Pteridium* communities have originated in the *dry* regions since 1920. Sharp edges to the bracken communities such as described for Breckland (**2**, p. 223) have been noticed, and are well marked where the *Pteridium* is advancing over almost bare, fairly uniform slopes or flats. Except against one plant *Pteridium* has had little opportunity of making use of its well-known power of competition, owing to lack of organised competitors. The exception is *Epilobium angustifolium* which quite early had covered extensive stretches of ground on the northern ridge. Here it is being invaded by *Pteridium*, the border line between the two communities being sharply defined. On examining the *Pteridium* numerous plants of *Epilobium* were found among it. Owing to its great height *Epilobium* is not so easily ousted by *Pteridium* by shade effect as other plants are. The flowering stems grow above the bracken and are thus in open daylight, but the shorter sterile stems and all the stems in the earlier stages are badly affected by the shading of the bracken. Although *Epilobium* sprouts before *Pteridium*, the latter soon overtakes it so that until the *Epilobium* shoots push through the curtain of fronds, they are in considerable shade. It is probable, however, that the reduction in nitrification correlated with the increase in acidity of the soil under *Pteridium* has a greater effect than the shading. *Epilobium* is a "nitrate-loving" plant (**7**, résumé, p. xliii), the luxuriance of its growth being more or less directly related to the nitrifying power of the soil, and estimations have shown that nitrification is less active under *Pteridium* than among the *Epilobium* outside the bracken community. Thus the willow herb will be gradually replaced by the bracken. This process is being followed in greater detail by means of selected quadrats.

Apart from *Epilobium* the *Pteridium* communities are remarkably pure, especially in the older parts where the action of the fronds has been continuous

over a longer period, except for young birches of all sizes which are to be found growing among the bracken.

Only a small portion of the higher ground is occupied by *Pteridium*, the remainder being the scene of struggles between other plants. We would wish to emphasise that all the dominant plants and most of the others as well are able directly to colonise the bare ground. It is first necessary that the pine litter should be partially decomposed by soil fungi and bacteria before the higher plants can obtain a foothold, but lower plants other than these play no necessary rôle as prime colonisers.

(*b*) *Calluna vulgaris* consocies.

The coloniser *par excellence* of the dry regions of the felled area is, as might be expected, the heather, *Calluna vulgaris*. Since the original Callunetum is on the far side of the unfelled pinewood very little help has come from that source; this explains the tardiness of the spread of *Calluna* at first. It was not until the surviving plants in the larger openings in the wood, or perhaps in the body of the wood itself, had recovered sufficiently to flower and produce the seed necessary for colonisation that any rapid spread took place: also it is probable that the pine-needle covering was at first not sufficiently decomposed. At present there are many plants which produce prodigious quantities of seed. The heather grows very quickly on such soil and is rapidly producing a continuous, if low, carpet of vegetation. The favourable conditions for growth are well exemplified in the very profuse flowering which in its turn produces more seed and fresh plants. The two photographs (Plate II, figs. 1 and 2) show the same view taken in 1922 and 1925 respectively.

Although in many places the new Callunetum is thick and from 9–12 ins. high, there is as yet little of the ground vegetation found in it elsewhere (cf. Part I). The mosses *Campylopus flexuosus*, *Webera nutans*, *Polytrichum juniperinum* and *P. formosum* are present in very small quantity under the heather: continued search failed to discover either *Hypnum cupressiforme* var. *ericetorum* or *Dicranum scoparium*, which are so frequent in the mature Calluneta. The first named is doubtless handicapped by its rare fruiting whereas *Polytrichum* fruits regularly so that the spores soon reach the newly covered areas. There are a number of localities on the felled areas where the presence of small pine trees up to 20 ft. in height and the absence of large stumps indicate the former presence of an opening in the mature wood. Here the typical Callunetum mosses mentioned above are found although in rather small quantity. Other relict plants found on these areas include *Lecidea granulosa*, *Hypnum schreberi*, *Cladonia furcata**, *C. sylvatica*, *C. uncialis*, *C. pyxidata*, *C. fimbriata* and var. *radiata*, and *C. coccifera**. Those marked with an asterisk do not occur in the pine openings, but are ordinary Callunetum species. Very few of the above are found in the young *Calluna* consocies.

FIG. 1. Dry area in 1922 showing invasion of *Calluna* consocies. Small birches can just be detected here and there.

FIG. 2. The same area as that shown in Fig. 1, taken from the same spot in 1925, showing increase of *Calluna* and great height growth of the birches.

Observations seem to show that *Dicranum* and *Hypnum* are spreading into the *Calluna* consocies from these relict areas.

An interesting feature in the embryonic Calluneta is the frequency of *Erica cinerea* (cf. **5**, pp. 156–163), this plant being much favoured by the comparative lack of competition and growing very well. Its prevalence is also probably due to its greater abundance in the mature pinewood, as described in Part I. In the more closed areas *Erica* is less common. From this and other observations it seems that the explanation of the distribution of *Erica cinerea* in heath communities must be sought in its relation to *Calluna* and not in terms of habitat factors directly. It is apparent that *Erica* is always dominated by *Calluna* under normal heath conditions, in all probability owing to the latter's taller growth, but that when the conditions become abnormal *Calluna* is often affected more than *Erica*; in these cases *Erica* becomes more abundant. Such abnormal conditions are reduction of light, eating by rabbits, disturbance of soil, drying out of soil, burning of heath, etc., and it can be seen that these may have an equivalent effect in that they affect *Calluna* more adversely than they do *Erica*. Most of them are certainly unfavourable for *Erica* itself. This question is being investigated more fully.

On the ridge, which is much more exposed and has much less soil, both *Calluna* and *Erica* are less common than elsewhere. The former is gradually creeping up the southern slope and should eventually dominate the ridge, but at present (1925) *Epilobium* is the most abundant plant there. *Erica cinerea* is, however, locally abundant on certain rather dry gravelly slopes, where it forms a low interrupted sward and flowers profusely.

(c) *EPILOBIUM ANGUSTIFOLIUM* CONSOCIES.

One of the most interesting of the phanerogams is *Epilobium angustifolium*, since it is practically absent from the original heathland. This species was first recorded by Mr W. J. Lucas on the felled area in 1918 and apparently was absent previously since it is too conspicuous a plant to be overlooked. *Epilobium* is particularly well adapted for colonising newly-bared areas since it produces an abundance of seeds which are carried long distances by wind. In addition it has extensive branched roots usually producing a number of adventitious aerial shoots. The latter grow very closely together, and are very tall, thus being able to shade over and crowd out other plants. Our germination experiments show that usually the seeds are not able to germinate in acid raw humus, but if this is removed the plant soon establishes itself.

Until 1921 the higher ground was covered with a thick (1–3 ins. = 2·5–7·5 cm. deep) layer of partially decomposed pine-litter except at the summit of the ridge. Here the organic covering was blown away at an early date, leaving the underlying gravel, and this was rapidly colonised by *Epilobium*. In some places the effect of exposure has been so much as to remove some of

the surface soil, the pine roots being totally exposed, but the *Epilobium* has maintained itself and is still very abundant.

It has been shown (**7**) that the presence of *Epilobium* is closely related to the capability of the soil to produce nitrates and that nitrates are stored up in the organs of the plant, especially in the younger stages; Hesselman terms *Epilobium* a "nitratophilous" plant. In coniferous woods with a raw humus layer on the ground nitrification does not take place, but on disturbing the ground or removing the humus nitrification is initiated. Such conditions are paralleled here, the general distribution of *Epilobium* being easily explained on this basis. Soil which has been burnt always nitrifies actively for some time afterwards, and Hesselman (**8**, résumé, pp. ci–cv) records *Epilobium* from all such places after fires. In 1921 fires burnt away the peat completely in many places, thus enabling *Epilobium* to colonise areas where otherwise it would not have succeeded. These fires will be dealt with more fully later.

The best growth of *Epilobium* on non-burnt areas is seen in certain hollows on the northern ridge. A considerable amount of gravel has been removed producing a large depression—named by us the "Great Hollow" and described fully later on—with a number of subsidiary holes in its proximity. The sides of these pits are very steep and unstable, fragments being carried down continually from above. They may be as much as 10 ft. in depth. Hesselman (**7**, pp. 370–373) has described the occurrence of *Epilobium* in gravel pits in Sweden and has shown that even in quite bare mineral soils nitrification proceeds actively but is increased if humus be mixed with the gravel, etc.; such conditions are almost exactly reproduced in these hollows. Estimations of the power of nitrification of soil by the phenol-sulphonic acid method were made in one spot at the base of a slope. On testing after allowing the moist soil to stand for 25 days the soil contained 133·5 mgm. NO_3 per litre of soil. In such places *Epilobium* grows very luxuriantly, some of the shoots being over 6 ft. in height, and completely crowds out any other plants which may be present at first. It is a curious fact that in the more open parts also *Epilobium* always grows preferably in slight depressions, so that in some places where the ground is regularly ridged there are long parallel rows of plants in the grooves with quite bare ground between them. Soil samples collected from the ridges and hollows were stored for 34 days and the nitrifying power of the soil estimated. The soil on the ridges consisting of sand with a slight admixture of humus gave 0·95 mgm. NO_3 per litre of soil, while the soil from the hollows, which was a black mild humus with birch leaves, etc., gave 53·76 mgm. NO_3 per litre of soil during the same period. This shows that in the hollows the soil is a much more favourable medium for nitrification than on the ridges and in view of Hesselman's work this seems to be the explanation of the distribution of *Epilobium* in this region. Nitrification estimations in other places, however, do not always show such clear differences and no

doubt other factors enter into the problem. This is being followed up in greater detail.

The *Epilobium* consocies differs from the others mentioned in its much shorter life, as the plant rarely maintains itself for very long in any given place. This is especially so of places where burning has taken place (see later) and is no doubt due in such cases to the re-establishment of the original unfavourable conditions when certain effects of the fire have disappeared. In the areas dealt with now which are unburnt the life of the consocies is longer and perhaps in places may be indefinitely prolonged, such places being, for example, on steep banks where fresh soil is continually being exposed.

(*d*) ASSOCIES OF *BETULA ALBA* AND *B. PUBESCENS*.

There are two other plants, besides those already dealt with, which form communities on the drier areas, viz. the two birches named above. Of these *B. alba* is decidedly the commoner on the dry areas; indeed *B. pubescens* is a rather rare plant there. This agrees with conditions in Epping Forest where Mr Paulson tells us that *B. alba* is more frequent on the higher and drier ground. There seems no reason for supposing that *B. pubescens* cannot grow well on dry areas since quite well-developed specimens, as healthy as any of those of *B. alba*, occur on the top of the North Ridge. Apparently it is in the seedling stage that the solution of the problem lies, plenty of seed of *B. pubescens* being available all over the heath. Unfortunately some germination experiments carried out in 1925 on the terrain in order to clear up this point were vitiated by the unseasonable drought in May and June of that year, and we have had no time to repeat the experiment. With respect to other factors we have few indications at present. Dr Salisbury suggests that *B. pubescens* grows better under more acid conditions than *B. alba*, but we can find nothing to support this at Oxshott, indeed the superficial roots of *B. alba* grow in a more acid medium in the dry *Calluna* consocies than do those of *B. pubescens* in the wet *Molinia* consocies. Mr Tansley's experience is that they grow equally well in very acid conditions, but that *B. alba* grows much better than *B. pubescens* under neutral or somewhat basic conditions, but of course we have no information bearing on that here since the lowest acidities obtained are *p*H 6·9.

Hybrids are very frequent at Oxshott and serve to increase the difficulty of effectively tackling the above problems; they occur occasionally on the dry areas.

As will be seen later, *Betula* colonises the damper areas more readily than the dry ones where in most places the trees are scattered at intervals of 10–50 yds. from one another. In spite of this there are several places where the birches are dominant or at least abundant. One such area is to be found N. and N.E. of Black Pond (Fig. 1). Here the ground is almost bare except for many young birches which are about 4–6 years old and up to 10 ft. (3 m.)

in height, forming a somewhat dense scrub. These birches must have colonised the bare ground here coincidently with the *Calluna* elsewhere: they are thus true pioneer colonisers.

The chief plant to be found between the young trees is *Calluna vulgaris* which is scattered about at intervals of several yards or more. On the typical developing *Calluna* consocies it is noticeable that attack by rabbits, of which there are a number on this part, is of little importance although there is ample room for penetration between the individual plants (**3**, p. 61). It is only at the edges of the *Calluna* zones that the effect of rabbit attack is at all evident. It seems that there are more *Calluna* bushes than can possibly be bitten to injure them appreciably; in fact in these areas young *Ulex nanus*, *Molinia* and *Carex pilulifera* seem to be the rabbits' first choices. This is not the case in the birch area described above. Here the amount of food is strictly limited, the *Betula* being too old, with the result that almost every heather bush is nibbled down to a compact circular cushion, flowering being almost entirely suppressed. In one or two places where the *Calluna* is rather thicker it was not eaten so much and was flowering freely. The isolation of the bushes is therefore a distinctly unfavourable condition and the lack of seed production probably explains the slow colonisation of this region. It is interesting to note that isolated *Erica cinerea* bushes in the same region were practically untouched and flowering profusely. *E. cinerea* is eaten in other places on the Common, but apparently is not so much appreciated as *Calluna*; in this region there is presumably enough of the more palatable *Calluna* to satisfy the relatively few rabbits present.

The reason for the occurrence of "pioneer" birch scrub in this area is probably the close proximity of many mature trees of *Betula alba* and the consequent availability of enormous masses of seed. In most other places where the dry areas are at all near mature trees these are actually themselves in wet areas and are predominantly *B. pubescens*, which species, as mentioned above, only establishes infrequently on the drier regions. There seems to be little difference in the state of decomposition of the pine humus here and elsewhere.

(*e*) General Observations.

Scattered over the drier area and found in all the developing communities there, with the exception of those of *Pteridium*, are the following plants:

Aira praecox		Molinia caerulea	
Betula spp. (seedlings)	f.	Ornithopus perpusillus	
Carex pilulifera		Pinus silvestris (seedlings)	l.
Cuscuta epithymum (on Calluna, Ulex nanus and Erica cinerea)		Rubus spp.	
Deschampsia flexuosa		Senecio silvaticus	
Erica tetralix	r.	Trifolium repens	
Fagus silvatica (seedlings) on ridge		Ulex europaeus (seedlings)	
Juncus squarrosus		U. nanus	

In addition there are several plants usually associated with excavation heaps and rabbit burrows only.

Anagallis arvensis	Polygonum persicaria
Cerastium vulgatum	Solanum nigrum
Cirsium arvense	Sonchus oleraceus
Poa annua	

The Common was used a little for military purposes during the war, and these plants were probably introduced then or during the felling; one or two (*Cerastium* and *Sonchus*) are commonly found on other parts of the heath and are, no doubt, constant immigrants from outside.

Among the plants of the first list there are some which offer points of interest. *Erica tetralix* and *Molinia* are found almost exclusively in the zones bordering on the wet series of communities. The latter in particular seems to be extending its range rapidly upwards on the higher ground. Isolated tussocks far from the main body of *Molinia* are thriving and have produced inflorescences up to 3 ft. in height during the past three summers. In these cases however the tussocks were growing apart from *Calluna*, *Molinia* probably not being able to compete successfully with *Calluna* in these dry districts. As mentioned above, *Molinia*, when growing isolated, also suffers from the attack of rabbits. On quite dry ridges small *Molinia* tussocks are found bitten right to the ground and this is, no doubt, a potent factor in preventing the spread of *Molinia* above a certain contour.

Ulex nanus has appeared, chiefly in the *Calluna* areas, where it is growing well in many places, producing upright and oblique shoots and flowering. In the shelter of birches it forms large bushes about 3 ft. high. In the barer parts it is early attacked by rabbits which keep on nibbling away the soft young shoots and thus keep it in close cushions. Fritsch and Salisbury (**6**, p. 135) note the rarity of establishment of seedlings at Hindhead and this corresponds with the slow spread at Oxshott since all the plants must have come from seed. *U. europaeus* seedlings are growing in several spots in the bare areas especially near Round Hill where the plant is common on original heathland.

Cuscuta occurred very abundantly both in 1922 and 1923, but less frequently in 1924 on the young *Calluna* bushes. It was also seen on *Erica cinerea* and *Ulex nanus*. In 1922 it did a considerable amount of damage to the bushes, but in 1923 the attack was not so severe. Although cases have been noted in which plants have died after an attack by *Cuscuta*, yet generally the damage is not so great and is usually limited to a complete or partial prevention of growth in size. Some plants seem to be attacked more or less regularly every year, others only occasionally.

Senecio silvaticus is a very characteristic plant of the partly bare regions where it often occurs in large clumps. It seems to prefer those places where the humus covering is thinner or absent, such as the vicinity of rabbit burrows. Apparently it is a "nitratophilous" plant like *Epilobium angustifolium* (**7**, résumé, p. xliii) and only occurs where nitrification is active in the soil. Its occurrence at Oxshott in similar places to those occupied by *Epilobium* is

therefore easily explained. It was first recorded in 1918 and has spread very considerably between 1922 and 1923, doubtless owing to its efficient means of dispersal. On the ridge it is restricted to depressions, probably because the seeds are all blown into the hollows, since in some of its stations lower down it is almost as much exposed to desiccation in the seedling stage; the explanation may perhaps be similar to that given above for *Epilobium*. *Senecio* is mainly a biennial plant, many seedlings appearing in the autumn of the year previous to flowering, but it may also be an annual. This, together with its relatively short flowering period and its lack of means of vegetative spread, renders it a much less efficient coloniser than *Epilobium*.

The species of *Rubus* occur in the form of low bushes which spread by means of creeping stolons in all directions. Several species are included in this category, but as no difference in procedure was noticed they are treated together.

In order to test the effectiveness of these stolons as a means of colonisation measurements were made from a number of these bushes. It was found that in February and March 1923 most of the plants had at least one stolon rooted, although the majority of the stolons were not. The following are distances from the root of the main plant at which stolons were found rooting:

Plant 1. 8 ft. 3 in.

Plant 2. 8 ft. 8 in. (to N.E.), 8 ft. 7 in. (to S.), 6 ft. 6 in. (to S.), 6 ft. 0 in. (to N.W.).

Plant 3. 9 ft. 5 in. (to W.), 7 ft. 6 in. two stolons (to N.).

It must be remembered that the actual lengths of the stolons were often greater as they do not always grow straight. In Plant 2 an unrooted stolon had reached the length of 14 ft. 5 in. (4·4 m.), while a young plant which had obviously originated from the older one was found 7 ft. 4 in. from the parent.

The area of Plant 2 was re-examined in the spring of 1925 and it was found that the two bushes recorded in 1923 had been converted into a large number of closely placed plants which are gradually matting together into a low tangle. The lengths of the stolons were again measured, the longest one found rooting being 10 ft. 10 in. (= 3·25 m.), while there were non-rooting stolons up to 13 ft. 2 in. in length. Both in 1923 and 1925 the majority of the stolons had rooted in heather bushes, although in 1925 a case was seen in which a stolon branched at the tip had rooted in several distinct places, all in the open, but one of them had actually forced its way between the bark and wood of a pine stump. However in most cases the stolons terminating in the open seemed incapable of rooting, possibly owing to animal attack or frost. The old stolons only maintain connection between parent and offspring for three years at the most—they are dead the last year—and after that time it is difficult to decide from what source a young plant has been derived.

It will be seen from the Plant 2 figures above that young plants may be produced in many directions at once: obviously *Rubus* is quite capable of

increasing rapidly in favourable localities. The seeds are presumably bird-dispersed in the first place; the species is thus being recruited continually from elsewhere. The plants themselves flowered and fruited in the summers of 1923 and 1924, and there is every reason for believing that many new ones have arisen by seed from the others nearby. It is noticeable here, as on the unfelled heath, that the bushes are commonest in the vicinity of rabbit burrows. This is doubtless due to the disturbance of the ground and removal of the unfavourable humus layer (cf. Part I, p. 294).

Where all the humus has been removed on the ridge by wind a hard rock-like surface of sand is often left. This is almost impossible to colonise except by vegetative growth from more favourable centres on the part of plants like *Epilobium* and *Pteridium*; it is therefore almost completely bare.

The following mosses occur on the drier felled areas, viz. *Bryum argenteum*, *Funaria hygrometrica*, *Polytrichum juniperinum*, *P. piliferum*, *P. formosum*, *Dicranum scoparium* and *Webera nutans*. None of these is at all common except on burnt ground. Under isolated birch trees or groups of trees thin carpets of the above mosses are sometimes found. On this moist substratum the large lichens *Peltigera spuria* and *Cladonia pyxidata* occur occasionally. The lichen *Lecidea uliginosa* occurs commonly on the peat in much of the drier region, especially in the *Calluna* zone. It is often the first coloniser in such places and seems to be an important factor in the production of surface "scale" owing to the binding action of the hyphae on the surface layer. Another lichen occurring in similar places, but by no means as commonly, is *Cladonia uncialis*; this however plays no part in the formation of surface scale. *Lecidea granulosa* also is found, rarely, in the *Calluna* consocies. Considered generally, the lower plants do not act as prime colonisers at Oxshott.

(II) *The Birch Phase.*

In addition to the pioneer communities of *Betula* described above there are seedlings and young trees of both species to be found everywhere, though never abundantly. These trees grow among the *Calluna* and *Epilobium* and more rarely in the Pteridietum. They are most frequent where the vegetation is sparser and do not seem to be able to invade the closed communities very easily. We may consider these to be the vanguard of the "Birch Heath" phase in the succession, but it is very difficult to say to what extent this phase will become established on the dry areas. In a few places, especially among *Epilobium*, the birch has grown so compactly as to produce open scrub, and in one or two places in slight depressions small birch thickets are found. The best example of the Birch Phase is to be found in the Great Hollow, and for this reason among others we give a more detailed account of it.

The Great Hollow. On the northern slope of the ridge is a large hollow which was probably first formed by digging for the gravel there. It dates from pre-pinewood times, as large pine stumps (90 years old) occur at its

bottom. The depression is about 100 yds. (90 m.) long, is in some places 20 ft. (6 m.) deep and has very precipitous sides except towards the north. The "Great Hollow," as we have termed it, is interesting because it shows the effect of protection on the nature and rate of colonisation of the felled regions. It is probable, judging from the ages and spacing of the felled trees that there was no more vegetation originally in the hollow than elsewhere, but now there is a very striking difference, the vegetation being very rich and varied, while the slopes outside are much barer.

The dominant vegetation consists of a scrub with large numbers of the two birches, *Betula alba* being much the commoner, and young trees of *Pinus*. In the spring (February) of 1923 the pines were mostly from 2 ft. 6 in. (76 cm.) to 4 ft. 6 in. (137 cm.) high, and were very close together in many places. The birches were rather taller, being up to 8 ft. (2·64 m.) in height on the same date, but a number of the tallest birches had been felled in the summer of 1922 so that really the birches were still further ahead. Where *Pinus* occurred in quantity *Betula* was not common.

In view of the question of succession from *Betula* to *Pinus* some measurements were made to see what were the annual increments in the lengths of the leading shoots of the two species and the percentage gains in a year. With *Pinus*, at the eastern end, the increments for 1922 were from 26–45 cm., an average percentage increase of 54·7, and in the centre in rather smaller trees the increments were 18–38 cm., an average of 40 per cent. *Betula* at the eastern end with increments of 60–115 cm., had an average increase of 71·5 per cent. These and the *Pinus* were of approximately equal ages (3–5 years). From the bases of the large birches felled in 1922 shoots of 166–193 cm. had developed. It can be seen that the growth of *Betula* is extraordinarily rapid, so that it will at first outstrip *Pinus*. This is in accordance with other accounts.

In early 1925 the ascendancy of the birches was very marked, the largest being up to 12 ft. or about 4 m. in height, in places forming an almost impenetrable thicket, but later in the year these were nearly all felled in connection with the replanting mentioned above. It was very noticeable how the social habit of the young pines completely prevented the growth of the birch locally.

Growing among the young trees and on the bottom of the Great Hollow generally is a well-developed carpet of *Calluna* and *Erica cinerea*. Around the edges, especially where the slope is steep, *Epilobium angustifolium* flourishes while *Pteridium* is dominant in a few places. The following is a general list for the Hollow made in 1922:

Betula alba (young)	a.—l.d.	Q. sessiliflora (young)	o.
B. pubescens (young)	o.—f.	Rubus idaeus	1 plant
Castanea sativa (young)	o.	R. fruticosus agg.	o.
Fagus silvatica (young)	r.	Salix cinerea	r.
Pinus silvestris (young)	l.d.	Sorbus aucuparia (young)	r.
Quercus cerris (young)	r.	Ulex europaeus and seedlings	o.
Q. robur (young)	o.		

Calluna vulgaris	f.—a.	J. squarrosus	r.
Carex pilulifera	f.	Lotus uliginosus	r.
Deschampsia flexuosa	o.	Molinia caerulea	r.
Digitalis purpurea	r.	Ornithopus perpusillus	r.
Epilobium angustifolium	l.a.	Potentilla erecta	r.
Erica cinerea	a.	Pteridium aquilinum	o.—l.a.
E. tetralix	r.	Rumex acetosella	r.
Galium saxatile	r.	Senecio jacobaea	r.
Hieracium pilosella	r.	S. silvaticus	r.
H. umbellatum	l.f.	Veronica officinalis	r.
Juncus effusus	o.		

Most of the plants were present only in very small numbers, as is quite evident from the lists. This is probably due to the time factor: they have not had time to get there yet in quantity. The majority of the typical heath plants are included in the above list and it is doubtful whether the list will be enlarged much in the future especially as the pines are growing rapidly. At present (1925) the list is quite complete; in fact several of the above species cannot now be found in the Hollow. The wholesale destruction of *Calluna* bushes by the shade of the closely placed birches was a striking feature noticeable on felling. There are one or two deeper hollows where water lies during the winter; it is here that the damp-loving types are found. In a general way it may be considered that the Great Hollow probably represents a stage of colonisation which will not be reached on the other parts of the dry areas for some years to come and is in that connection of especial interest.

(III) *The Pine Phase.*

The above facts are particularly important in relation to the "Pine phase" which one would naturally expect to follow the "Birch phase," but in the Great Hollow the succession has been telescoped and the pines have appeared very early. In this area, in addition to the sheltered conditions in the Hollow, an important factor is the presence of a clump of unfelled pines just near. These have sown seed since 1917 and there are numerous young pines on the north slopes of the ridge around the clump. Also on the very crest young stunted fasciated pines are found, although there the conditions are not at all favourable for the establishment of *Pinus*, the soil being bare and stony. Elsewhere on the dry areas young pines are very infrequent; it is probable that the critical point is at the development of the first foliage leaves or perhaps even earlier. In the course of some experiments in which pine litter from the pinewood was placed on certain areas, a number of pine seeds germinated, but all the seedlings died away some time after the above-mentioned stage although at first they looked quite healthy. In most of the region in July, when *Pinus* germinates, the higher exposed ground is usually very dry and not favourable. Perhaps with the increase in the plant covering now taking place *Pinus* will find more advantageous conditions. The observations given above, however, seem to show that the lack of seed supply is a very important and perhaps the deciding factor.

(IV) *General Remarks.*

The scheme of colonisation on the drier parts of the felled areas may therefore be represented as follows, the double lines indicating the more important lines of development (see Fig. 3). What follows *Epilobium* seems to be largely a matter of chance since apparently it is not capable of remaining indefinitely in a region, but rather depends on colonisation of new areas for its success. It is therefore replaced by various plants according to different circumstances.

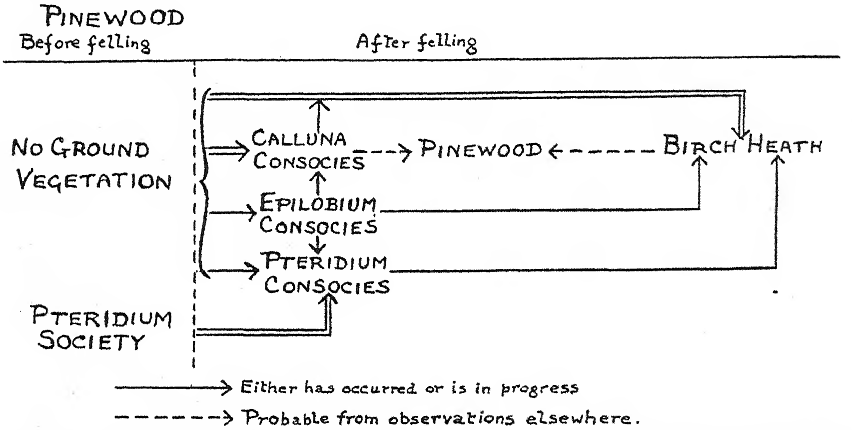

FIG. 3. Scheme of colonisation of the dry areas. Double lines indicate the more important lines of succession both in this and in later diagrams.

It is very interesting to note that young seedlings of *Betula* can establish themselves in Pteridietum of moderate thickness, a fact which had been suspected previously on the unfelled areas, but it is doubtful if colonisation of really luxuriant Pteridietum ever takes place. It is an important point that according to our observations the thickness of the bracken in a given place fluctuates, possibly due to the temporary accumulation of autotoxins and thus during the period of minimum thickness the birch may get established. Afterwards its very rapid growth enables it to compete with the *Pteridium* for light.

Information as to some of the later stages of the above scheme is of course lacking, so we can only make suggestions as a result of observations on the original heathland and from other heaths.

B. DAMP SERIES.

On the lower and wetter parts of the felled area the progress of recolonisation is quite different from that already described, the dominant plants here being *Molinia*, various species of *Juncus* (*J. effusus* and *J. conglomeratus* in particular) and *Betula* spp. Partly owing to the greater water-content leading to more favourable conditions generally, and partly to the presence of *Molinia*

in the original pinewood, the colonisation has proceeded more rapidly and would be at a much more advanced stage still were it not for the disastrous fires of 1921.

In the lower regions the soil is in many respects different from that on the higher parts. In all cases there was still a considerable peat layer on the surface and although much of this has been removed by the fires yet in no place has the humus been entirely blown away as on the ridge. Again, owing to the greater initial and subsequent water contents the pine-humus has decayed more rapidly than on the drier areas, giving place to less acid peat layers of *Molinia*, etc., while surface scale is entirely unknown. The almost continuous moist condition of the surface layers also allows of more effective germination and establishment. All over the relatively unburnt regions—scarcely any of the lower part of the heath was entirely untouched by the 1921 fires—there is now a peaty layer one or more inches (over 2·5 cm.) in thickness while in places where there were bogs in the original pinewood the peat is somewhat thicker. The drainage in large areas of the low-lying parts has, since 1920 at least, been very defective in spite of the numerous drains cut, there being many large pools of water which are more or less permanent throughout the winter.

Another point of interest which is of importance in its bearing on the later stages in the succession is the fact that the damp areas are peripheral to the felled region and thus in close contact with unfelled woodland around. As a result of this many more disseminules fall on the damper parts than on the dry ones. The total result of all the factors mentioned above is the much more rapid colonisation of the damp areas as already stated.

(I) *Primary Communities.*

There are no true pioneer communities on this part of the Common as the soil was already occupied by some sort of ground vegetation previous to felling. *Molinia* was present in a very stunted condition over most of the damper parts of the wood and on felling this rapidly sprouted anew, forming a coarse herbage in 1918. By 1920 the *Molinia* herbage had been transformed into a tall tussock grassland with innumerable inflorescences.

Perhaps the most striking feature of the felled areas in early 1921 was the great stretches partially or wholly dominated by *Molinia caerulea*. This is evident from the map (Fig. 1). It is useful to note that the boundary of the *Molinia* consocies marks the upper limit of the damp type communities in practically all parts, corresponding usually to a definite contour on the terrain. However, where there are broad transitional regions the delimitation of damp and dry series is difficult. Unfortunately the fires in 1921 interfered greatly with the course of colonisation. In many places a quite new succession has been initiated following these fires; this will be dealt with later. Over a great deal of the ground, however, the burning was not severe enough to

exterminate the dominants, which have recovered again: probably the succession here, although delayed several years, is in the main not much altered.

The primary communities can be divided into several types which are on the whole related to the drainage; other factors also enter the arena in places and cause modifications. In this "water-content series," passing from the driest to the wettest, one finds (*a*) *Molinia* consocies, (*b*) *Molinia-Juncus* ecotone, (*c*) *Juncus associes*. In addition to these are areas with *Sphagnum* sub-dominant on the site of old bogs in the pinewood and better considered as a relict community (*d*).

Immediately below the dry series or transitional communities (see below) *Molinia* occurs, with some *Calluna* and *Erica tetralix*, and then gradually *Juncus* appears more and more abundantly, until at the lowest levels almost pure communities of *Juncus* occupy the ground.

At an early stage in the development of these communities seedlings of *Betula* appeared, but it was some time before the birch phase was reached in most areas. This topic will be dealt with later. Nevertheless isolated trees or small clumps were scattered throughout the dominant *Molinia* or *Juncus*.

(*a*) *Molinia* consocies.

In 1920–1922 this community covered large stretches in the centre of the lower parts of the Common, where the ground was most free from colonisation by the birch. Apart from the young trees the community was strikingly uniform in appearance, consisting of large tussocks growing close together and producing inflorescences up to 3 ft. 6 in. (1 m.) high. Around the pine-stumps, where there was a thicker layer of organic material, there were often considerable bare spaces, but otherwise the vegetation was closed. The chief associates of the *Molinia* were *Calluna* and *Erica tetralix*, the latter being especially abundant locally, while *Calluna* was commoner nearer the upper edge of the community. Since 1920 these two species have increased greatly on the drier upper levels: this rather supports the suggestion made in Part I (**11**, p. 295) that pure *Molinia* communities are rarely found on such heaths, the mixed type of community being more frequent. It is probable, at any rate we know no example to the contrary, that permanent Molinieta do not exist on heaths in the low rainfall districts of England. Where the drainage is good the *Molinia* is replaced by other herbaceous or dwarf-shrub species, while on damper soils woodland is soon established. *Molinia* communities therefore only appear as a stage in succession after felling or perhaps burning. *Juncus effusus* is frequently found along lines of drainage and represents outliers of the wetter type communities.

On the lower levels species of *Juncus*, and damp-loving forms in general, are much commoner, although *Molinia* is still usually dominant. Water often lies about in pools during the winter, and soil analyses show that, allowing

for organic matter, the water-content is on the whole rather high even where spots are chosen away from large clumps of *Juncus*. In one place in this zone among almost pure *Molinia* the water-content two days after rain in March 1922 was 423 per cent. of the dry weight in the surface peat layer—this soil did not appear at all wet—and figures between 150 and 200 per cent. are not infrequent. In summer the area is drier, but the average water-content of the sub-peat layer is then about 25–30 per cent. of the dry weight.

Subjoined is a general list of species for the *Molinia* consocies, made in June 1922, but it must be remembered that the fires of 1921 in all probability exterminated the rarer species.

Young trees and shrubs.

Betula alba	o.—f.	Sorbus aucuparia	r.
B. pubescens	f.—a.	Rhododendron sp.	v.r.
Castanea sativa	o.	Rubus fruticosus agg.	o.
Ilex aquifolium	v.r.	Salix cinerea	o.
Pinus silvestris	o.	Ulex europaeus and seedlings	r.—o.
Populus alba	r.	Quercus robur	o.—f.

Dwarf shrubs and herbs.

Agrostis alba	o.	E. tetralix	f.—l.a.
Anthoxanthum odoratum	o.	Eriophorum angustifolium	r.
Calluna vulgaris	o.—l.a.	Holcus lanatus	r.—f.
Carex binervis	o.—l.f.	Hypochaeris radicata	o.
C. goodenowii	o.	Juncus acutiflorus	r.
C. hirta	r.	J. bufonius	o.
C. muricata	r.	J. conglomeratus	o.—f.
C. pilulifera	r.	J. effusus	r.—l.a.
C. stellulata	r.	J. squarrosus	o.—f.
C. vulpina	r.	J. supinus	o.—f.
Cirsium arvense	r.	Lotus uliginosus	r.—o.
Cuscuta epithymum (on Calluna)	l.	Luzula congesta	o.
Deschampsia flexuosa	r.	L. multiflora	o.—l.f.
Drosera longifolia	v.r.	Molinia caerulea	d.
Eleocharis palustris	r.	Potentilla erecta	o.—l.f.
Epilobium angustifolium	r.	Pteridium aquilinum	o.
E. hirsutum	r.	Polygonum hydropiper	r.
E. montanum	o.	Rumex acetosa	l.
E. palustre	o.	R. crispus	r.
E. tetragonum	o.—f.	Scirpus caespitosus	r.
Erica cinerea	v.r.—r.	Teucrium scorodonia	r.

It will be noticed that most of the above species are far from common; indeed they rarely affect the uniform appearance of the *Molinia*.

With the phanerogams in the *Molinia* consocies grow a number of bryophytes, some of which may be considered as relict from the pinewood, while others have probably come in since felling. None of them is very common although some can usually be found under the *Molinia*, etc.

Catharinea undulata	Leucobryum glaucum
Ceratodon purpureus	Marchantia polymorpha
Dicranella heteromalla	Mnium hornum
Dicranum scoparium	Polytrichum commune
Hypnum cupressiforme var. ericetorum	P. juniperinum
Lophocolea cuspidata	Webera nutans

Hypnum ericetorum probably survived from the pinewood in the shelter of *Molinia*: it will be remembered that it does not occur on the drier parts; it was probably killed after felling by exposure on the dry bare ground.

(*b*) *Molinia-Juncus* ecotone.

This occupies a belt of varying width between the drier *Molinia* and the wetter *Juncus*, the two plants being usually in equal quantities: *Juncus effusus* and *J. conglomeratus* are the two most important rushes. The community is typically developed where the water content of the soil is relatively high but the drainage is fairly good, as along the larger drains. The associated flora is intermediate between that of the *Molinia* consocies and the *Juncus* associes, damp-loving species having higher frequencies than those given in the above list. There are also a few additional species, viz. *Cirsium palustre*, *Hydrocotyle vulgaris*, *Viola palustris* and *Scutellaria minor*.

The following is a list of the plants found in the *Molinia-Juncus* ecotone.

Agrostis alba	a.	J. effusus	f.—c.d.
Anthoxanthum odoratum	o.	Lotus uliginosus	f.
Athyrium filix-foemina	r.	Luzula congesta	o.
Calluna vulgaris	o.	L. multiflora	o.
Cirsium palustre	f.	Molinia caerulea	a.—c.d.
Dactylis glomerata	r.	Myosotis caespitosus	l.
Epilobium angustifolium	r.	Potentilla erecta	f.
E. palustre	o.	Ranunculus flammula	r.
Erica tetralix	f.	R. repens	l.f.
Hieracium umbellatum	r.	Scabiosa succisa	o.
Holcus lanatus	f.—l.a.	Scrophularia aquatica	r.
Hypericum pulchrum	r.	Scutellaria minor	o.—l.f.
Juncus conglomeratus	f.—a.	Viola palustris	o.

(*c*) *Juncus* associes.

Juncus was very rare in the wood before felling, being nearly restricted to the environs of Black Pond. Possibly the series of communities mentioned above represents different stages in the invasion of the *Molinia* consocies, which had a start in the race after felling, by species of *Juncus*. It seems probable, however, that complete replacement of the *Molinia* will not take place at the higher levels, even if it does elsewhere. Burnt patches in this region have been filled in some places with numerous *Juncus effusus* seedlings during 1923, showing that the conditions are not unfavourable for this species in the absence of competition. At the lower levels it would find even more congenial surroundings, and observations seem to show that here an actual increase in *Juncus* is in progress.

In the lowest portions and especially where the drainage is rather imperfect extensive areas dominated by *Juncus* occur. The most important species are *Juncus effusus* and *J. conglomeratus*, but in certain places *J. acutiflorus* is co-dominant or dominant, and *J. supinus* also occurs, while many marsh plants which are only rarely found in the *Molinia* consocies are common here. Throughout the winter the *Juncus* areas form an almost impassable

swamp, the standing water being often over a foot (30 cm.) deep, but in summer a great deal of this swampy region becomes quite dry. On the whole the *Juncus* associes is not so readily colonised by birches as the *Molinia* consocies, probably owing to the unfavourable nidus for germination offered by the thick tussocks of crowded upright stems and leaves. Thus the *Juncus* regions at the present time (1925) are generally more open and free from scrub.

The following plants occur in the *Juncus* associes:

Agrostis alba	o.—l.a.	J. supinus	o.—f.
Anthoxanthum odoratum	r.	Lotus uliginosus	o.
Calluna vulgaris	v.r.	Luzula congesta	o.
Carex stellulata	l.	L. multiflora	o.
Deschampsia caespitosa	r.	Molinia caerulea	o.—f.
Erica tetralix	r.—o.	Ranunculus flammula	o.
Holcus lanatus	o.—l.a.	Scutellaria minor	o.
Hydrocotyle vulgaris	o.	Betula alba	r.—o.
Juncus acutiflorus	r.—l.d.	B. pubescens	r.—l.f.
J. conglomeratus	a.—c.d.	Salix cinerea	o.
J. effusus	a.—c.d.	Polytrichum commune	f.—l.a.

(*d*) *SPHAGNUM* BOGS.

As mentioned above, there are several places on the felled area where *Sphagnum* occurs in quantity, in places becoming sub-dominant. Associated with the bog moss may be either *Molinia* or *Juncus* spp. or more often a mixture of these. From information received it appears that the *Sphagnum* bogs are those which existed prior to felling, so one may perhaps consider that *Juncus* has outstripped *Sphagnum* in the invasion of new areas. The above remarks receive support from the fact that the only stations on the heath for *Narthecium ossifragum* are in the *Sphagnum* bogs. The Bog Asphodel is by no means restricted to such localities on other heaths, so one can only conclude that it has not yet spread into the more recently formed swamps. With *Sphagnum* is also found *Aulacomnium palustre*, sometimes very abundantly.

The full list of plants occurring in the *Sphagnum* bogs is as follows:

Agrostis alba	f.	Juncus supinus	o.
Calluna vulgaris	o.	Lotus uliginosus	r.
Carex stellulata	f.	Luzula congesta	o.
Cirsium palustre	r.	L. multiflora	o.
Erica tetralix	o.—f.	Molinia caerulea	a.—c.d.
Holcus lanatus	o.	Narthecium ossifragum	l.
Hydrocotyle vulgaris	f.—a.	Potentilla erecta	o.—f.
Juncus acutiflorus	f.—a.	Scutellaria minor	o.
J. conglomeratus	o.	Typha latifolia?	r.
J. effusus	f.—c.d.	Viola palustris	o.

Mosses.

Aulacomnium palustre	f.—a.	Leucobryum glaucum	o.
Campylopus flexuosus var. uliginosus	f.	Polytrichum commune	f.—a.
	r.	P. juniperinum (on mounds)	o.
Hypnum fluitans var. falcatum	o.	Webera nutans var. longiseta (c.fr.)	f.
H. stramineum	l.a.		

Mosses (continued).

Sphagnum aquatile var. remotum (floating)	r.	S. cymbifolium var. glaucescens	l.a.
S. auriculatum var. canovirescens (c.fr.)	a.—l.s.d.	S. inundatum	r.
S. compactum var. squarrosum	r.	S. molluscum var. vulgatum (c.fr.)	l.a.
var. semisquarrosum	l.f.	S. plumulosum var. remotum (floating)	o.
S. cuspidatum var. plumosum (floating)	r.	S. obesum (usually floating)	l.a.
		S. recurvum var. majus	l.s.d.

Hepatics.

Gymnocolea inflata	a.	Calypogeia fissa	a.
f. laxa	r.	C. trichomanis	r.
Cephalozia bicuspidata	a.—l.s.d.	Lepidozia setacea (c.fr.)	l.f.
C. connivens	o.	Lophozia ventricosa	r.

Lepidozia occurs in some of the bogs as fine threads binding *Sphagnum* stems closely together, and also sometimes in compact tufts on the ground. Two rather striking absentees are *Leptoscyphus anomalus* and *Odontoschisma sphagni* which are usually characteristic of such bogs.

Zonation of the bryophytes can be detected in the *Sphagnum* bogs, the Sphagna themselves showing it most distinctly. The following zones were distinguished by Mr Richards, Zone I being the highest and Zone IV the lowest.

I. Sphagnum molluscum var. robustum
S. compactum var. squarrosum
var. semisquarrosum.

II. S. cymbifolium var. glaucescens
S. compactum var. subsquarrosum
S. molluscum var. vulgatum
S. recurvum var. majus
S. auriculatum var. canovirescens.

III. S. plumulosum var. remotum
S. recurvum var. majus
S. auriculatum var. canovirescens
S. inundatum

IV. S. obesum
S. aquatile var. remotum
S. crassicladum var. intermedium
S. plumulosum var. remotum.

(e) Drains.

Crossing the felled area there are a large number of drains which vary in size and water supply. Some have permanent streams of running water, others stagnant water in winter only, while yet others are moist in winter only and quite dry in summer. These drains are either shaded to various degrees by young birches or tall *Molinia* or are quite open. Their banks are always more or less sandy, but the floor of many is clayey.

As the conditions in different ditches and in different parts of the same ditch are so varied, the flora also varies greatly in abundance and richness, but in most cases there is a thick carpet of mosses and hepatics on the banks; in this are imbedded small phanerogamic plants. Lichens are almost entirely wanting. On the bottoms of the ditches species of *Juncus* are often abundant.

Of these the most characteristic is *Juncus supinus* f. *fluitans* which is either completely submerged or floats; with this is a floating form of *Agrostis alba*. The only true water plant is *Potamogeton polygonifolius*, this being, however, restricted to the larger drains.

The following examples from Mr Richards give an idea of the variation in the lower plants (Table I):

Drain 1. On edge of wet birch-scrub. Banks very damp, sandy and deep with permanent stream. Shaded.

Drain 2. In *Molinia* consocies north of North Ridge. Moist in summer, a little stagnant water in winter. Banks of peaty sand. Unshaded.

Drain 3. In drier *Molinia* consocies. Dry in summer, moist in winter. Banks sandy, mostly shaded.

Drain 4. In upper part of *Molinia* consocies, near middle of Common. Banks very dry, shaded by thick bramble bushes.

Table I.

		1	2	3	4
On banks					
Mosses:	Sphagnum cymbifolium var. glaucescens	r.	—	—	—
	S. compactum var. subsquarrosum	—	o.	—	—
	S. recurvum var. majus	r.	—	—	—
	Polytrichum commune	—	—	—	o.
	Ceratodon purpureus	—	—	o. (c.fr.)	—
	Dicranella heteromalla	a. (c.fr.)	—	v.a. (c.fr.)	o.
	Mnium hornum	—	o.	—	—
Hepatics:	Pellia epiphylla	o.	—	—	—
	Cephalozia bicuspidata	a.	v.a.	a.	—
	Calypogeia fissa	l.a.	f.	f.	f.
	Lepidozia setacea	—	f.	—	—
	Diplophyllum albicans	—	—	—	f.
Lichens:	Cladonia pyxidata	—	—	o.	—
On floor					
	Sphagnum obesum	o.	—	—	—
	S. crassicladum var. intermedium	—	—	—	o.

In addition to the above the following have been found in ditches at Oxshott: *Calypogeia neesiana*, *C. trichomanis*, *Cephalozia lammersiana* (c. per.), *C. connivens*, *Lophozia excisa*, *Lophocolea cuspidata* and *Dicranella cerviculata* (teste Mr W. R. Sherrin). *Pellia epiphylla*, *Cephalozia bicuspidata* and *Dicranella heteromalla* are the most characteristic species.

These drains are very rapidly colonised by plants, as was shown in the case of one re-cut and widened early in 1922 on the south edge of the damp region. On April 29th there were already a few plants of *Pellia*. The ditch was again examined in February 1923, the following plants being found.

At the top of the sides were *Dicranella heteromalla* and *Polytrichum commune*.

On the sides further down:

Calypogeia fissa	a few stems	Dicranella heteromalla	o.
Juncus supinus	f.	Pellia epiphylla	o.
Pinus silvestris	1 seedling	A Sphagnum belonging to the *subsecundum* group	a few tufts
Potentilla erecta	1 plant		

On the bottom in running water was *Juncus supinus* f. *fluitans* (f–a).

The bulbils of the latter—it is usually pseudo-viviparous—are swept along by drainage water; this may explain the rapid colonisation of the ditch. Of the hepatics *Pellia* and *Cephalozia* fruit freely, this being an important factor in producing their wide distribution. In the drier drains *Pellia* is uncommon; here *Dicranella* and *Cephalozia* are co-dominant.

A further examination in March 1924 showed that colonisation had been still more rapid since the previous year. The banks in many places bore large patches of mosses and hepatics, *Dicranella heteromalla*, *Calypogeia trichomanis* and *Cephalozia bicuspidata* being the chief species in the upper portions, while *Pellia* often occurred in a line just above average water level. In one section of the ditch *Diplophyllum albicans* was quite dominant. In the ditch itself were many plants of *Juncus supinus* f. *fluitans* and also scattered individuals of *J. effusus*, the former also growing up the sides in places. *Erica tetralix* was the commonest of the other phanerogams, seedlings and young plants being present all along the sides, mainly near the top. Other plants found were as follows:

Blechnum spicant	1 plant	Polytrichum commune	spreading from top
Calluna vulgaris (seedlings)	o.	Hypnum cupressiforme var. ericetorum	a few stems
Pinus silvestris (near top)	r.	Aulacomnium palustre	1 tuft
Potentilla erecta	o.	Funaria hygrometrica	1 tuft on a twig
Rubus sp. (trailing)			
Sphagnum cymbifolium group	o.		

In 1925, although no detailed survey was made it was noticed that the sides were completely covered with mosses and hepatics while large tufts of *Juncus* half choked the bottom of the ditch. Other plants not noticed before were *Betula* (seedlings), *Molinia* (not common but spreading from top) and *Agrostis vulgaris*. It can be seen that the higher plants are the species occurring in the surrounding *Molinia* consocies and birch scrub. In this part of the ditch phanerogams were not so common as in the more open parts.

(*f*) Black Pond.

This can scarcely be termed a part of the felled area, but it seems advisable to describe it here for three reasons: (1) it has been influenced by the felling of the pinewood around; (2) it forms the lowest member in the series of communities from dry to wet conditions; (3) it acts as a centre for the survival of aquatic forms, which can invade any temporary pools formed in the felled area in the vicinity.

Black Pond (see map, **11**, p. 289) is a large pool at the western end of the valley in the felled area. A fringe of trees was left around the pond until 1921 when those on the southern side were felled, those on the north and west being untouched. The eastern end tapers to the inlet where it connects with the main drainage of the valley. On the western side is an embankment designed to hold back the water and although it has been broken in several

places the level of the water inside is still higher than the low ground outside. Much of the pond has dried up as a result of these breaks and is now occupied by a marsh which is inundated in wet weather only.

At the inflow end there is a large area of marshy ground dominated by *Juncus effusus* with *J. acutiflorus* forming an almost pure community in the northern part. This is probably the focus from which the *Juncus* invasion mentioned above is taking place. The main N. and S. path crosses the inflow by a bridge which tends to hold up the water. By the inflow stream west of this bridge *Juncus effusus* is again dominant: on either side of it is a zone of *Eleocharis palustris*, *Eriophorum angustifolium* and *Agrostis alba* co-dominant, these grading into the *Molinia* consocies on drier ground; willows (*Salix cinerea* and *S. fragilis*) occur among the rushes. To the north of the pond the ground rises rapidly, so that on this side the zonation is sharp and some of the zones are lacking. At the western end is a large irregularly shaped sheet of open water, but most of the pond is filled with a tall reed-swamp of *Phragmites vulgaris* which grows either in the water itself or on ground which is dry during the summer. On the north *Phragmites* comes right up to the bank: on the south it was burnt away by the 1921 fires and replaced temporarily by *Eriophorum angustifolium*. In 1925 the *Phragmites* had partially recovered in this region, there being scattered haulms about 2–3 ft. (60–90 cm.) in height. Here, as well as in the drier parts of the reed swamp, many young trees of *Betula* are growing and the whole will ultimately pass into woodland.

A transect across the pond in 1921 gave the following zonation (Fig. 4).

Reed Swamp. Near the open water in the centre this is almost pure *Phragmites*—*Typha latifolia* occur in one place on the western side—but where the ground is relatively drier there are a number of other plants growing among the stems of the reed. They are:

Betula alba	o.—l.a.	Hypochaeris radicata	r.
B. pubescens	o.—l.a.	Juncus acutiflorus	o.
Eleocharis palustris	o.	J. effusus	o.
Epilobium angustifolium	r.	J. supinus	f.
Eriophorum angustifolium	f.—a.	Molinia caerulea	o.
Hydrocotyle vulgaris	f.	Viola palustris	r.
Hypericum elodes	r.		

Some of these are obviously invaders from the dry areas around. In the water itself where it comes to the bank is *Scirpus fluitans*.

The following Sphagna grow in the reed swamp, usually in the wetter parts, especially where the ground rarely dries out.

Sphagnum plumulosum var. remotum	l.a.	(in water up to c. 10 cm. deep)
S. cuspidatum var. plumulosum	l.a.	(water from c. 5–30 cm. deep)
S. obesum	a.	(water from c. 25–30 cm. deep)
S. franconiae (probably only a form of S. obesum)	a.	(water from c. 25–100 cm. deep)

The last named grows abundantly in the reed swamp and as large floating masses in the open water beyond, as well as more sparingly in some of the neighbouring ditches. *S. recurvum* forms large beds almost

entirely at the eastern end of the pond. *S. cuspidatum* var. *plumosum* grows characteristically in small scattered groups in shallow water, especially in small pools separated from the main pond in summer. None of the Sphagna of the upper zone of the damp series occurs around Black Pond.

The following Bryophytes occur in the area with much *Eriophorum* on the south side of the pond or elsewhere.

Aulacomnium palustre	f.	Sphagnum serratum (Mr W. R. Sherrin)	
Cephalozia bicuspidata	f.	S. amblyphyllum	o.
Hypnum fluitans var. falcatum	f.	S. recurvum var. majus	l.a.
Sphagnum papillosum var. normale (comm. Mr W. R. Sherrin)			

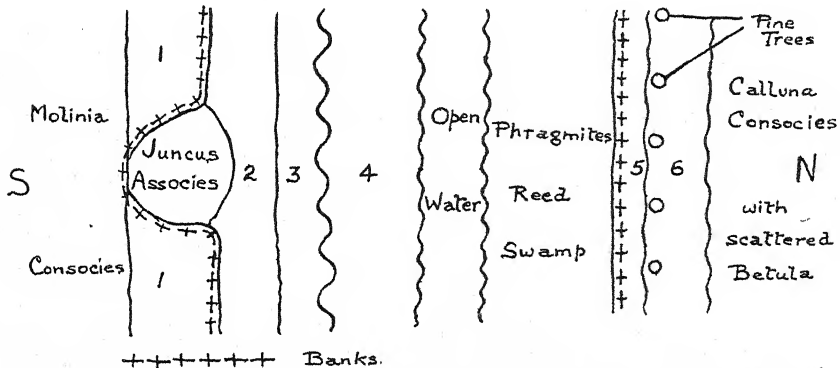

FIG. 4. Diagram of belt transect across Black Pond from N. to S. to show zonation of communities. 1. *Molinia-Juncus* ecotone. 2. *Eriophorum* and *Agrostis alba*. 3. *Eriophorum* and *Phragmites*. 4. Reed swamp of *Phragmites*. 5. *Agrostis alba*. 6. *Molinia* consocies.

It is obvious from the ordnance maps that this silting up of the pond and invasion by reed swamp, etc., has been in progress for many years. Even in 1912 there was very little open water, but it is probable that the reed swamp was in much deeper water then. In any case the felling of the surrounding wood has accelerated the process by increasing evaporation while the blocking of the drainage in the valley farther up has reduced the amount of water inflowing.

(II) *The Birch Phase.*

Since we first visited the district in 1920 active colonisation by *Betula* has been taking place so that now there are all gradations between close birch-scrub with undergrowth of *Molinia*, etc., and open *Molinia* with few birches.

Where the *Molinia* consocies is in close contact with plantations containing birches, or near mature birches left after felling, the area is rapidly being converted into birch scrub. On the east of the Common is a large circular felled region, termed by us the "Inner Circle" (see map, **11**, p. 289). When we first visited this in 1920 it consisted of typical *Molinia* consocies with a number of small birches about 18 in. (45 cm.) high. At the upper (southern)

margin was a zone of almost bare ground with scattered and even smaller birches. In 1923 the lower part was still predominantly *Molinia*, but the birches there were from 4–5 ft. (1·2–1·5 m.) in height while the upper portion, including the originally bare zone, had been converted into a thick birch scrub nearly 7 ft. (2·1 m.) in height. In the upper portion were also numerous pine seedlings of various sizes. There have been several superficial fires in the region during this period but except in the south-west corner they have had little effect on the colonisation. This region is surrounded by mature birches and pines on most sides and this explains the rapid invasion. In 1925 the conditions were much the same but the scrub in the southern half was very tall and thick while there were quite tall pines (up to 6 ft. = 1·8 m.) among the birches.

In other regions the birch scrub was even better developed, but unfortunately most of it was destroyed by fire in 1921. Nevertheless the birch has made a wonderful recovery in these regions and the scrub is almost as thick as previously. As will be seen from the map, the most prominent belt of scrub occurs around the periphery of the felled area and then gradually thins out towards the centre.

In certain damper parts of the pinewood prior to felling there were a number of small *Castanea*, Birch and other trees under the pines. When the latter were felled the *Castanea*, etc., grew well, forming a scattered scrub in these parts of the developing *Molinia* consocies. It is probable that this *Castanea* zone, which occurs typically on the southern edge of the felled areas (see map) represents the distance to which *Castanea* had invaded the pinewood from the great plantation adjacent. It was shown previously (**11**, p. 298) that *Castanea* is able to establish itself under *Pinus*—germinating seeds and young plants have been found—and it is almost certain that it was not planted here since the pinewood was subspontaneous, although in the woods around planting was carried out. Many of the chestnut trees were badly damaged or killed during the fires so that this zone is not now so prominent, but the taller isolated trees still stand out amidst the more recent thick birch scrub.

As the trees grow up the ground vegetation becomes gradually suppressed, so much so that the ground is often almost bare under the young trees. *Calluna* is usually the first victim, while *Molinia*, *Juncus* and *Erica tetralix* persist longer, but even they become etiolated and do not flower. *Betula* casts a deeper shade than is usually ascribed to it in books, particularly in the young stages when the lower branches grow horizontally only a few inches above the ground. Later on, as the trees grow up, their growth becomes more open and a certain amount of recolonisation takes place, but in thick birch scrub *Calluna* and *Erica tetralix* never regain their lost positions.

In the damp regions *Betula pubescens* becomes co-dominant with *B. alba* or even outnumbers it, especially in the wetter places. Very few new plants

seem to be associated with the development of the birch scrub. Young trees of *Castanea*, *Quercus robur*, *Q. cerris*, *Sorbus aucuparia*, *Fagus silvatica*, *Prunus avium* and *Pinus silvestris* are dotted about, but in general the ground vegetation is simply an impoverished and stunted *Molinia* or *Juncus* associes.

In a few places the felling was not complete, sometimes owing to the relatively high proportion of deciduous trees originally present. In these regions conditions are rather different from those in the completely felled areas as seeds of these species are available in large quantities. A number of mature trees of *Betula*, *Quercus*, *Castanea*, *Fagus*, etc., were left scattered about and within this region a scrub has rapidly formed. Young trees of *Quercus* and *Betula* predominate, but other species occur. The ground vegetation is a mixture of *Pteridium*, *Molinia* and *Rubus* growing together in inextricable confusion and obviously in active competition—probably all survivors from the original wood. This scrub will in time be converted into Mixed Wood of the usual type, and possibly illustrates a further stage in the march of colonisation, the younger stages of which occur on other parts of the felled region. Few pines have yet appeared here.

(III) *The Pine Phase.*

Indications of a future development of this are much more evident on the wet areas than on the dry ones. Young pines occur abundantly among the *Molinia* and in the birch scrub, especially in regions abutting on the unfelled pinewood or on plantations containing pines, and there seems no doubt that another pine colonisation is in the first stages of development. At present, with the exception of several small clumps of pines from openings in the original wood and not felled with the other trees, none of the trees is over 10 ft. (3 m.) in height, and few exceed 5 ft. 6 in. (1·65 m.), representing trees eight years of age which appeared the year after the felling. Other trees of all sizes from 3 in. (7·5 cm.) upwards occur, and are in most cases thriving except where they are slightly etiolated owing to shading by the birches, or in the very wettest places. *Pinus* apparently does not succeed in soil in which the saturation point is maintained for any length of time, such conditions resulting, in the case of the larger plants, in an extraordinarily slow rate of growth, and in the seedlings dying at about two or three years of age.

Unfortunately *Pinus*, owing to its resinous tissues, suffered more severely than almost any other plant in the fires, otherwise it would be much commoner than it is. Since the crop which germinated from seed left after felling was mainly killed by fire, it is now left to wind to carry seeds into the interior of the felled area, and apparently wind, in spite of R. Smith's observations (**10**), is not a particularly effective agent of dispersal in the case of *Pinus*. At any rate the number of seeds carried more than 100 to 150 yds. (90–135 m.) from mature trees is not sufficient in view of the activity of agents destroying

the seeds and seedlings after dispersal. In the course of some sowings *in situ* carried on in 1925 something of the effect of these destructive agents was seen. A detailed map of the pine seedlings on part of the damp areas was made early in 1925, and it was surprising how few young plants (under 5 years) there were outside a radius of 130 yds. (117 m.) from the edge of the unfelled wood or from other mature trees. There seems no doubt however that, given a reasonable freedom from fires, especially during the next few years—larger trees are not so susceptible as younger ones—*Pinus* will gradually recolonise the wet areas and reconvert them to pinewood.

(IV) *General Remarks.*

The succession on the damp areas may be expressed in the following scheme (Fig. 5).

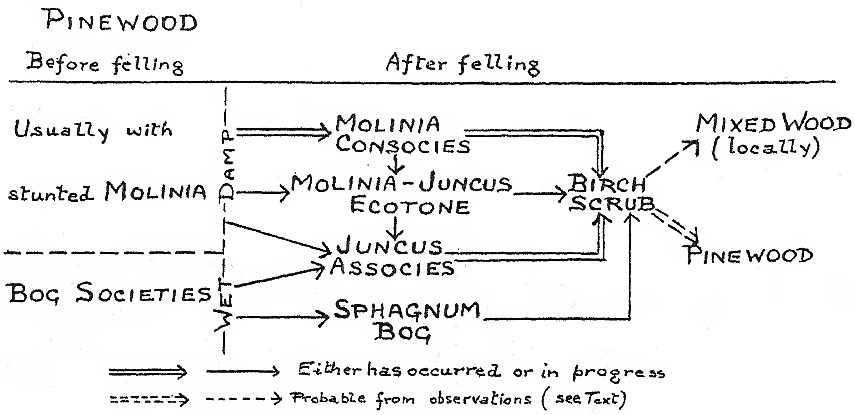

FIG. 5. Scheme of colonisation of the damp regions.

In all probability the *Juncus* and *Sphagnum* communities will not become colonised very quickly unless the drainage is improved. *Betula* can tolerate very great extremes of water content in the seedling stage, but the conditions among *Juncus* and *Sphagnum* with a thick layer of rotting saturated litter on the ground are not favourable for germination. This was well seen in an area adjacent to a well-developed birch wood on the east side of the Common. Although seedlings by the hundred occurred among *Molinia* and mixed *Molinia* and *Juncus*, yet in an almost pure zone of *Juncus effusus* nearer the wood hardly a seedling was to be seen. As mentioned above, *Pinus* is practically never successful in such localities.

C. TRANSITIONAL REGIONS.

In several places the sharp line between the wet and dry series communities is not present. This is due to the gradual slope from the higher to the lower ground resulting in a wide transitional zone, in which the dominants of the two adjacent types are in active competition. It has already been mentioned

that *Molinia* is apparently invading the *Calluna* areas in many places, probably owing to the blocking of the drainage leading to a higher water table and possibly to other factors. On the gentler slopes this affects a much wider zone than elsewhere, while at the same time the effect itself is not actually so noticeable.

The largest transitional areas seem to be those in which *Pteridium* and *Molinia* are the competitors. We have not been able to determine exactly what is happening here owing to the slow rate of change, but some observations a little lower down bear on the subject. Along the main drain in the valley is a high bank made from the excavated earth on which *Pteridium* is well developed. Away from the bank however it occurs only on the mounds around the pine stumps, the intervening spaces being filled with *Molinia*. Since *Pteridium* almost always reproduces vegetatively here it is reasonable to suppose that these patches represent the remnants of a once continuous stretch of *Pteridium* in the wood prior to felling, especially as decayed *Pteridium* rhizomes are found under the *Molinia* between the stumps. Since felling the water table has been raised and *Pteridium* has only been able to survive on the mounds around the trees. *Molinia* is therefore freed from *Pteridium* here, and it seems likely that the same is happening further up although more slowly.

Calluna, on the other hand, grows quite well in the damper parts, and therefore can maintain itself against *Molinia*. *Erica tetralix* is now appearing in quantity in the transitional *Molinia-Calluna* zone, and at the base of the *Calluna* consocies proper. The zonation here from above downwards is as follows:

(1) *Calluna* consocies.
(2) *Calluna* consocies—damp type with much *Erica tetralix*.
(3) Mixed community of *Molinia*, *Calluna* and *Erica tetralix*.
(4) *Molinia* consocies.

The communities here are thus coming into line with those on the original heathland (cf. Part I, pp. 291, 295). *Erica cinerea* occurs very rarely in this region though common enough among *Calluna*, while *Erica tetralix* finds its usual upper limit in the transitional zone, occurring but rarely in the dry regions proper.

Seedlings of *Betula* seem to grow more readily in the intermediate zones than in either the *Molinia* or *Calluna* consocies. The junction of wet and dry series is therefore often marked by a line of birch scrub. Possibly the medium water content together with the reduced competition from *Molinia* produces rather favourable conditions, since similar belts of scrub are found where *Molinia* abuts on almost bare parts of the higher ground. As one passes from the higher to the lower regions it is in these transitional belts of birch scrub that *Betula pubescens* first appears common.

The course of succession in these areas naturally resembles in certain respects those on both dry and damp areas, the most striking feature being perhaps the early appearance of the birch phase.

2. TERTIARY SUCCESSIONS (RECOLONISATION OF BURNT AREAS)

Although the whole of the changes following the felling of the wood should rightly be termed "secondary successions" or subseres, according to Clements' nomenclature (**1**), yet we have thought it advisable to use the term "tertiary successions" for successions arising from causes not in any way directly related to the felling, and thus subordinate to the main subseres studied. The chief and perhaps only series of "tertiary successions" (used in the above sense) taking place at Oxshott are those resulting from fires, mainly the disastrous ones of 1921.

On the original heathland the surface peat is formed from plants already there and is apparently not very inimical to their growth. On the felled area there is, on the other hand, a thick layer of pine-needle litter and peat which is very difficult of colonisation by plants until a certain stage in decomposition is reached. The removal of this by fire therefore not only alters the chemical properties of the soil as on ordinary heath areas, but it also involves the disappearance of this retarding factor. On the damper ground decomposition of the needles takes place more rapidly and was probably well advanced before the fires occurred.

From observations made late in 1920 and in the spring of 1921 it was evident that fires had occurred previously: in fact the débris from the felled trees was burnt after felling. A good many of the drier areas had still a thick layer of peat early in 1921, but charred stumps were present locally. In June and July 1921 a series of fires swept almost the whole of the felled areas, and these fires continued or were intermittent during much of August, some of the ground being burnt over several times. Rainfall records show that although rain fell in small quantities during June (0·29 in.), July (0·40 in.) and August (0·72 in.), it was not until September 11th when 0·90 in. fell that there was enough to wet the ground sufficiently to prevent further fires. Actually the fires mostly died away before this from lack of combustible material. The above figures however show how dry everything must have been.

On the drier areas the peat layer was completely removed over large stretches, especially at the western end of the north ridge where the underlying sand was exposed. In this region were many young birches which were all killed. The fire swept right along the south side of the ridge, but missed the "Great Hollow" except in one place. Further along parts of the *Pteridium* communities were completely destroyed and in a few places the *Calluna* also. Generally speaking, however, the latter was not continuous enough to enable the fire to spread easily, while bare sand here and there prevented extensive burning of the peat.

In the wetter parts the effect of the fires was devastating. Over much of the *Molinia* region, especially south of the main drain, the dominant was entirely killed, while everywhere it was badly damaged. Usually the patches

of killed and damaged *Molinia* alternated frequently, the burning often being worst around the pine stumps. The *Castanea* trees were very badly damaged, many of them failing to sprout until 1923, while some quite large trees were completely killed. The birches were severely injured, being exterminated in many places and extensive tracts of birch scrub were entirely consumed. A thick layer of charred materials was left everywhere. The very wet *Juncus* communities suffered less, but even they were sometimes killed, while the *Phragmites* in Black Pond was half burnt over. As others have noted (**6**, p. 118), the courses of fires are very capricious, and no doubt some areas were burnt several times while others were either missed altogether or were burnt very slightly.

A. Dry Regions.

In dry regions the recovery, except in one particular, has been very slow.

1922. In April numerous seedlings of *Epilobium angustifolium* were seen in depressions on the ridge; these grew up and flowered in the same year. In some places the birches sprouted, but generally they were entirely killed. *Pteridium* sent up a few scattered fronds of small size in many places, and was perhaps on the whole less affected than any other plant. Some of it however was completely killed and has shown no sign of life since. Digging in this area revealed dead, decaying rhizomes—probably killed by the heat. In addition to removing the peat layer the fire had so hardened the sand beneath that locally it was almost like rock, this being very inhospitable ground for germinating seeds. On terrain of this type *Hormidium flaccidum* was found in a thin macroscopic green layer.

1923. Little change had taken place in some of the burnt regions but in others the birches had sprouted quite successfully and seemed to have recovered completely, while *Pteridium* was growing much as before the fire. *Epilobium* had spread very considerably, covering large areas. On the northern slope of the ridge *Funaria* was growing well in extensive patches, but had not fruited: it is interesting to note that the same stage was reached on the damp areas in 1922. *Bryum argenteum* was also seen in a few places and fruited in October. *Hieracium pilosella* and *Rumex acetosella* were noticed here and there, but the latter was not so common in the dry regions here as on other heaths. Seedlings of *Senecio silvaticus* appeared late in the year.

In one place at the base of the dry area all the burnt plants of *Ulex nanus* had sprouted from the stools, while the other members of the original *Calluna* consocies here had been killed. *Ulex* was therefore dominant, which it otherwise never is (**5**). The exposed bushes were nibbled into cushions by rabbits, while the plants in the shelter of small birches were large and flowered profusely.

1924. This year *Ceratodon purpureus* appeared in quantity for the first time on the dry areas, replacing *Funaria* in many parts; in others, however, *Funaria* was still the dominant moss. *Epilobium angustifolium* also continued

FIG. 1. Dry area. Birch as the prime coloniser on burnt ground. *Epilobium angustifolium* can be seen in the middle distance. Soil between plants perfectly bare. Oct. 1925 (see p. 235).

FIG. 2. Damp area. Burnt patch in *Molinia* consocies with carpet of *Polytrichum* and many young bushes. Oct. 1925 (see p. 239).

its spread and formed in some parts thickets some 3 or 4 ft. (90–120 cm.) in height. Later on in the year many seedlings of *Calluna* and *Betula* grew up under the shade of the willow herb. Birch and heather seedlings also appeared in the barer burnt patches, while locally *Senecio silvaticus* was abundant, flowering profusely. Other plants found included *Sonchus oleraceus* and *Taraxacum officinale* (both common weeds of non-acid soils around), their growth being no doubt favoured by the less acid soil reaction.

In several places, however, the development was not so far advanced. On the north slope of the ridge there were in November extensive carpets of *Ceratodon purpureus* mixed with *Polytrichum formosum*, in which birch seedlings were decidedly rare, while *Epilobium* was present only as scattered clumps. The advent of the *Polytrichum* marked a further stage in the reversion to the original acid substratum.

On the regions in which the surface had been burnt quite hard an interesting extra phase had been interpolated, and here was seen almost the only example on the Common of a cryptogamic phase being necessary before the higher plants could colonise the ground. Darker patches of this hard surface were found on investigation to be damper than the normal owing to the presence of a thin film of mucilaginous soil algae. On these patches there appeared afterwards *Ceratodon* and *Polytrichum*, but in 1924 very few higher plants arrived. The mosses were not seen on the ordinary baked surface.

1925. No marked change had taken place up to September of this year. *Epilobium* was maintaining itself on most of the areas, although it had certainly decreased in luxuriance. *Polytrichum* had replaced *Ceratodon* in many places, and many young plants of *Betula* (Plate III, fig. 1) and *Calluna* had established themselves. *Pteridium* commenced to recolonise the burnt areas around the remnants left by the fire.

General Remarks. It may be seen that on the drier burnt regions the re-establishment of the original vegetation has commenced, but has not yet progressed far, while temporary communities still hold the field in most places.

B. Wet Regions.

1921. Where the *Molinia* was only moderately burnt it recovered quickly, a short thick turf being produced by the autumn after the fire, but no flowers. Seedlings of *Epilobium* and *Senecio silvaticus* appeared on the quite bare patches.

1922. The *Molinia* sprouted, producing inflorescences about a foot (30 cm.) high. *Betula* and *Quercus* also sprouted everywhere while a few plants of *Castanea* showed signs of life.

Meanwhile on the perfectly bare areas a rapid colonisation set in. Many seedlings of *Epilobium* appeared and those both of this species and of *Senecio* from the previous year flowered. This rapid appearance and spread of *Epilobium* and *Senecio* was no doubt due to the increased nitrification in the soil

following burning (see pp. 210 and 213). At the same time the ground became green with moss protonema, mainly of *Funaria hygrometrica* which developed and in a few places fruited; by July some of the previously bare patches were completely covered with this moss. Kessler (**9**, p. 369) has shown that the spores of *Funaria* will only germinate in an alkaline medium; this is provided for them by the salts in the ash left after the burning of the humus and litter. *Ceratodon purpureus* was also present but in very small amount. Annual plants such as *Rumex acetosella* appeared in great numbers, while many plants of *Deschampsia flexuosa* had arrived in parts of the burnt Molinietum.

In July in the drier parts of the *Molinia* consocies numerous seedlings of *Calluna* appeared, while in one or two districts a large number of seedlings of *Digitalis purpurea* sprang up. The origin of these is a mystery, as there were none flowering on the heath, but they probably came from a garden since in 1923 some had white flowers: the nearest garden was however a long way off. Other phanerogams which were observed on the burnt patches in 1922 were *Cerastium vulgatum*, *Epilobium montanum*, *E. roseum*, *E. tetragonum*, *Erigeron canadense*, *Hieracium pilosella*, *Holcus lanatus*, *Hypochaeris radicata*, *Rumex acetosella*, *Sagina subulata*, *Senecio silvaticus*, *S. vulgaris*, *Sonchus oleraceus*, *Stellaria media*, *Taraxacum officinale*, *Trifolium dubium* and *T. repens*, most of which are common weeds with excellent means of seed dispersal.

At the edges of the completely burnt patches there was a slight slope, and here a number of sporelings of *Pteridium* appeared. Apparently the conditions of moisture, etc., due to the hygroscopic nature of the layer of charred organic material present were suitable for the production of prothalli. *Polytrichum commune* and *P. juniperinum* arrived after *Funaria* especially in the wetter parts of the burnt patches, while *Marchantia* appeared locally in large quantities.

Taken as a whole, it may be said that apart from *Epilobium* the main development was by lower plants, mosses being most prominent. Owing to the greater moisture these get established much more quickly than on the usual dry type of heath. The first of the series of quadrat charts (Fig. 6) gives an idea of the condition of a typical completely burnt area in 1922, the scattered *Epilobium* plants being about 2 ft. (60 cm.) high.

1923. The mosses spread more, a great deal of the original burnt out ground in February being converted into green carpets of *Funaria* and *Polytrichum*, the former fruiting everywhere; *Bryum argenteum* was only common locally. *Polytrichum piliferum* appeared and *Ceratodon purpureus* fruited in many places. Later on in the year this moss became much more prominent and had apparently replaced *Funaria* in many places. This phase usually occurs after burning, when most, but not all, of the salts from the wood-ash have been washed out of the soil. *C. purpureus* is a moss noted for its extraordinary range of habitat and indifference to soil constitution; for instance, it grows well on both chalky soil and peat, though perhaps it has a preference

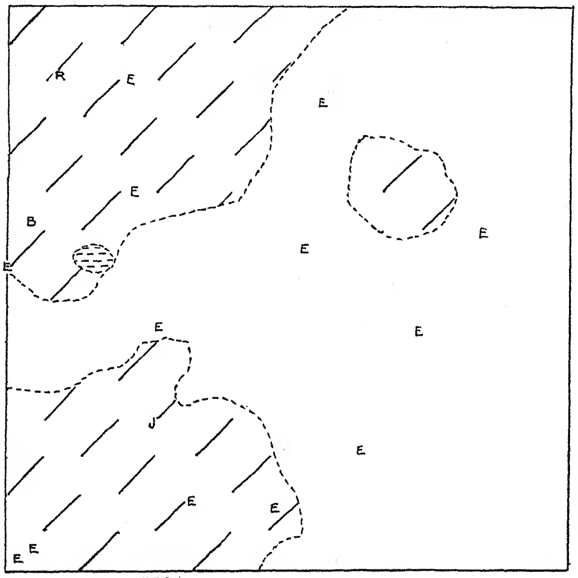

FIG. 6. 1922.

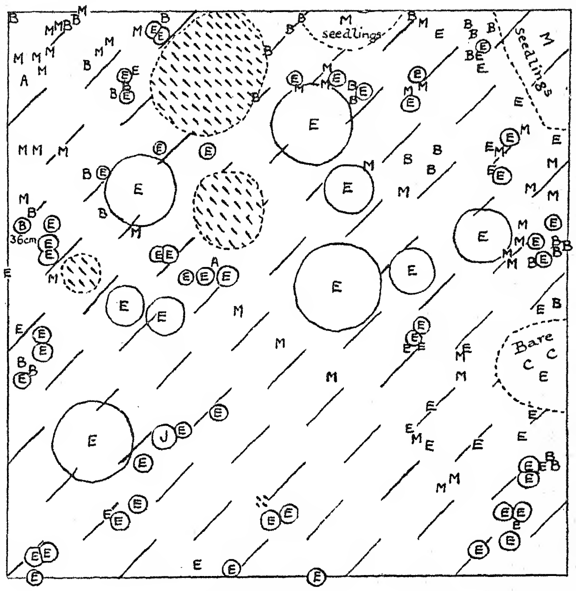

FIG. 7. 1923.

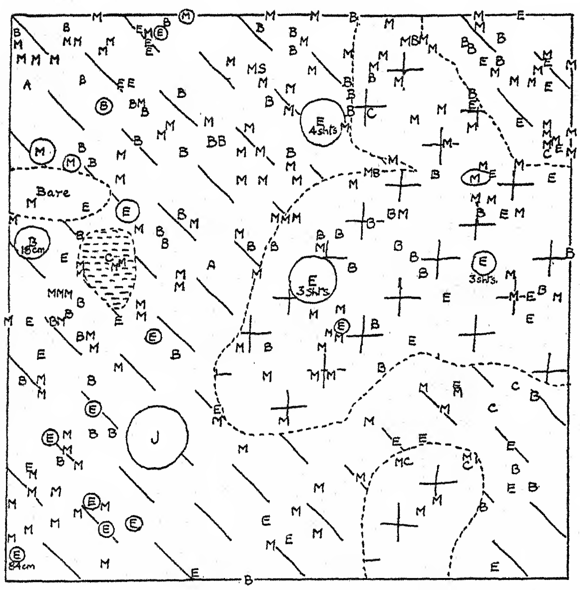

FIG. 8. 1924.

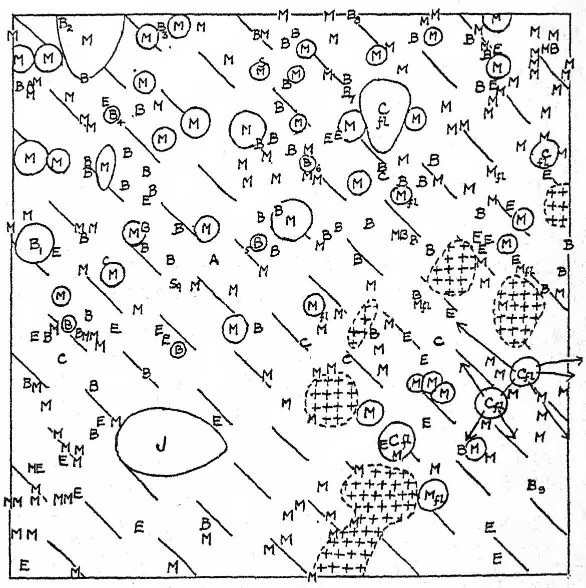

FIG. 9. 1925.

These are charts of the same quadrat made in the years 1922–25. The quadrat is 1 square metre in area. The following symbols, etc. are used in all the charts. Single letters represent seedlings or small shoots; the circles or other outlines indicate the areas of the larger plants, the number of shoots being given in some cases; the heights of certain plants are also given.

A., Sorbus aucuparia. B., Betula spp. *C., Calluna vulgaris. E., Epilobium angustifolium. J., Juncus conglomeratus. M., Molinia caerulea. R. Epilobium roseum. S., Salix cinerea. Sq., Juncus squarrosus.* = = = = *Marchantia polymorpha.* /// *Funaria hygrometrica.* + + + + *Ceratodon purpureus.* \\\\\\ *Polytrichum* spp. (mostly *P. juniperinum* and *P. formosum*).

FIG. 6. The *Epilobium* here was about 60 cm. high.

FIG. 7. A thick growth of *Epilobium* approx. 1 m. high filled the quadrat although the stems seem scattered in the chart.

FIG. 8. *Epilobium* almost as tall but much thinner.

FIG. 9. Tallest *Epilobium* shoot inside quadrat = 58 cm. B_1 7 shoots, highest 34 cm., B_2 30 cm., B_3 23 cm., B_4 24 cm., B_5 16 cm., B_6 22 cm., B_7 3 shoots, 10 cm., B_8 21 cm., B_9 2 shoots, 16 cm. Arrows indicate prostrate branches. *fl* = flowering.

for neutral and acid soils. As it is such an abundant species and fruits so readily, its spores must always be present in the atmosphere in a district like Surrey, and as the soil becomes less suitable for *Funaria* it becomes more so for *Ceratodon*. *Marchantia* also continued its spread. In the burnt areas in both years many fruit bodies of *Laccaria laccata* were seen, together with other rarer species.

The most striking development however was that of the phanerogams. On the partially burnt areas *Molinia* grew to its normal size and, in the damper areas particularly, produced inflorescences up to 3 ft. 6 in. (1 m.) in height. *Betula* also grew very well and seemed to have recovered completely, while a large number of *Castanea* trees which had shown no life in 1922 sprouted at the bases of the trunks.

On the burnt patches *Epilobium* was easily dominant, filling the drier places with a close vegetation 3–4 ft. (*c.* 1 m.) high, while later in the year the air was a mass of flying seeds which became entangled in everything. Many seedlings of *Betula* on the drier parts, and of *Molinia* and *Juncus effusus* on the damper, grew up during the year, while in some of the wetter regions *Holcus lanatus* was extremely abundant. Seedlings of many other plants also appeared, such as *Erica tetralix*, *Calluna*, *Deschampsia flexuosa*, *Juncus squarrosus* and *J. supinus*, these being members of the regular heath flora. The annuals and biennials, including various weeds, *Senecio silvaticus*, *Rumex acetosella* and *Digitalis* also increased in amount. *Aira praecox* and *Senecio jacobaea* were fresh arrivals in 1923.

Fig. 7 shows the same quadrat one year later (1923). The dominance of *Epilobium* is apparent, the willow-herb in this patch forming a thick stand over 3 ft. (*c.* 1 m.) high. The arrival of seedlings of *Betula*, *Molinia* and *Calluna* is evident.

1924. In this year the inauguration of two fresh phases in the succession could be seen. In the first place *Epilobium angustifolium*, which was quite dominant in many burnt patches in 1923, began to lose ground. Most of the plants were decidedly less luxuriant and showed a xerophilous structure normally associated with later phases in a burn succession. Other work done by us on *Epilobium* shows that this can be definitely related to the decrease in available nitrates.

In addition a great number of seedlings of *Molinia* and *Betula* could be found everywhere growing beneath the *Epilobium* and forming the vanguard of the next phases. At the same time *Polytrichum* spp., mainly *P. commune* and *P. juniperinum*, appeared in large quantity, *Ceratodon* being less conspicuous though still plentiful, while *Funaria* was banished to drier knolls where the succession was not so far advanced. Polytricha always become abundant when the last traces of the soluble salts in the ground have disappeared and the soil reverts to its former acid condition.

In the very wet parts *Juncus effusus* and *J. conglomeratus* had entirely

filled the burnt patches with a thick growth of young plants, while several of those which had appeared in 1923 produced small inflorescences. In one area, where the completely burnt region was more continuous than usual, *J. effusus* now formed an almost pure stand where formerly *Molinia* had predominated. The other members of the normal *Molinia* consocies also increased, some of them being very abundant locally.

An interesting feature in 1924 was the appearance on the damper burnt patches, especially those on which *Polytrichum commune* was dominant, of numerous seedlings of *Pinus silvestris*. Some of these no doubt grew up in 1923, but they were first noticeable in the following year, being then from 3 to 9 in. (8–23 cm.) in height. Many however seemed to be rather unhealthy, and probably will not survive, at any rate not in the wettest places.

Fig. 8 shows the state of colonisation of the same quadrat in 1924. The decrease of *Epilobium* and the increase in the other plants is very striking, also the almost complete dominance of *Polytrichum* spp.

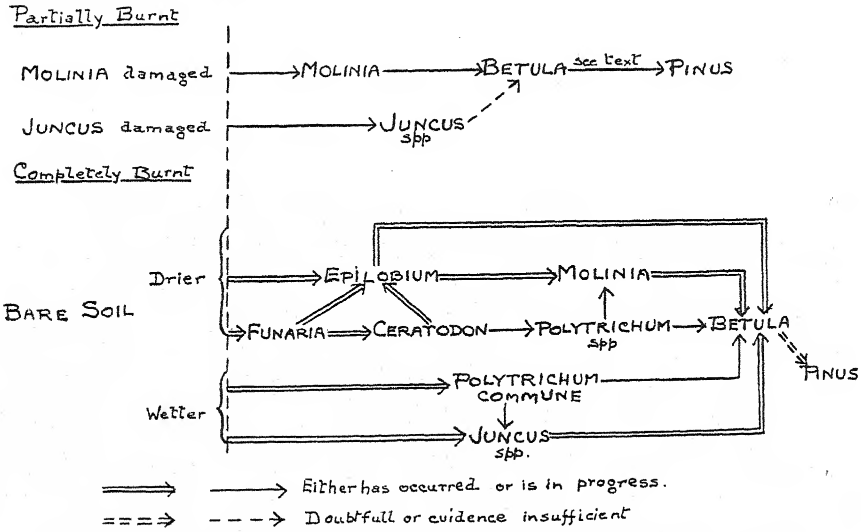

FIG. 10. Scheme of secondary successions following burning on the damp regions.

1925. The changes noted in 1924 were carried farther this year. *Epilobium* had almost entirely disappeared from many burnt patches, while many low thickets of young birches up to 18 in. (45 cm.) in height had grown up, these being very prominent in the less wet regions (Plate III, fig. 2). *Polytrichum* spp. (*P. formosum* and *P. juniperinum*) were almost entirely dominant in these places. On the wetter parts *P. commune* was the chief moss, usually associated with *Juncus* spp. Birches were abundant here also, although perhaps not in such large numbers as on the drier patches. *Molinia* had also increased greatly while *Calluna* was common locally. The fourth quadrat chart (Fig. 9) shows the state of a typical burnt region in 1925 and illustrates

some of the above points. It can be seen from the foregoing that the species of the typical wet soil community are quickly asserting themselves and that colonisation is extremely rapid. The sequence of colonisation on the damper burnt areas so far as it is known is represented schematically in Fig. 10.

In many places, owing to the rapid growth of birches on the burnt patches, the *Molinia* phase will become telescoped, the other communities passing direct into birch scrub. Where, however, the burns are away from the mature birches the *Molinia* consocies is re-establishing itself quite successfully. The initiation of the pine phase is also evident, though it will be some time before the pines will be of any importance on the burnt patches.

3. COMMUNITIES OF SPECIAL HABITATS

Under this heading we class communities which cannot be brought into a general scheme elsewhere.

(*a*) *Ruderal Communities*. There are places where the direct influence of man has greatly modified the vegetation and often made it possible for species alien to heath conditions to flourish. The track along the north end of the Common has been reinforced with clinker and earth and as a result a number of weeds and other plants are to be found there. Some of these have spread in places into the felled area adjacent and are there competing with the heath flora. In other places similar plants are found by smaller paths. In 1922 the following "weeds" occurred:

Arctium lappa		Ranunculus repens	
Cirsium arvense	f.	Rumex crispus	f.
C. lanceolatum	f.	Sonchus oleraceus	
Hordeum murinum		Stellaria media	
Lotus corniculatus		Taraxacum officinale	
Potentilla reptans		Trifolium repens	
Plantago lanceolata		Tussilago farfara	
P. major		Urtica dioica	
Polygonum aviculare		Veronica serpyllifolia	
P. hydropiper	f.	Vicia sativa	
Prunella vulgaris			

Polygonum hydropiper is typically found by paths in many places; its presence is probably correlated with the increased water-content due to trampling of the ground; the seeds may also perhaps be distributed in the mud on boots. Some of the above species, e.g. *Cirsium arvense* and *Rumex crispus*, are always found in waste places on the heath. There are also several rubbish heaps on the felled areas, especially a large one in the Great Hollow. On these were found various weeds and other plants. The following which have appeared in the Great Hollow at various times give an idea of the flora of these heaps:

Atriplex patula	Polygonum persicaria
Capsella bursa-pastoris	Populus alba (young)
Cerastium vulgatum	Senecio silvaticus
Chenopodium album	Sonchus oleraceus
Corylus avellana (young)	Taraxacum officinale
Digitalis purpurea	Teucrium scorodonia
Erigeron canadense	Veronica arvensis
Mahonia aquifolium	

An interesting addition was *Epilobium angustifolium* which by 1924 had completely overrun the above-mentioned large heap, this again being an example of its preference for spots rich in available nitrogen.

A rather exceptional habitat is the large heap of sawdust (50 yds. = 45 m. long and several feet thick in the middle) in the north-west corner of the heath: other heaps occur elsewhere. This sawdust is apparently a very inhospitable substratum for plants, since even in October 1923 practically nothing but a few small birches could be found on it. At the edges *Molinia* was trying to push through, but looked rather unhealthy. By October 1925 only a few seedlings of *Erica tetralix* had been added. That the sawdust becomes a suitable habitat later on is shown by the fact that a small mound (6 ft. × 4 ft. and over a foot deep) in another place had *Cirsium arvense, Anagallis arvensis, Solanum nigrum* and *Cerastium vulgatum* growing on it—a typical weed flora. Hesselman (**8**, résumé, p. c) states that sawdust on partial decomposition nitrifies actively and that nitratophilous plants then occur on it. The wood of *Pinus*, owing to the large amount of resin present, seems much more resistant to micro-organisms than other woods, and this accounts for the slow rate of decomposition of the Oxshott sawdust. In November 1923 on one sawdust heap the fungus *Tremellodon gelatinosum* was abundant.

(*b*) *Pine Stumps*. The stumps of the felled trees, which are scattered fairly regularly over the whole area, have a somewhat special flora which is composed mainly of fungi. At first, owing to the resinous nature of the wood and general unsuitability of the surface, the stumps remained bare. Later on the bark especially gradually decayed and many fungi were found growing on it or between the bark and the wood itself. The following have been found:

Corticium albo-stramineum		Polyporus amorphus	
Flammula sapinea	a.	P. hispidus	
Fomes annosus		P. mollis	
Hypholoma fasciculare	a.	P. tephroleuca	
Lenzites saepiaria		Polystictus versicolor	
Merulius tremellosus		Sparassis crispa (mostly on burnt stumps)	
Paxillus involutus		Thelephora laciniata	f.
Pholiota spectabilis	f.	Trametes gibbosa	
Pluteus cervinus (albino form)		Tremellodon gelatinosum	

In addition to these were *Polyporus schweinitzii* with *Hypholoma* and *Thelephora* on the roots. On the cut surfaces, especially associated with the holes of wood-boring beetles, *Calocera viscosa* and *Dacryomyces* sp. were found. The myxomycetes *Lycogala epidendrum, Fuligo septica* and *Stemonitis* sp. occurred plentifully both on the wood and on the bark.

Mosses also appeared at a fairly early stage although not frequently. The following have been found, mostly on the bark or on rough parts of the cut surface where a little mineral matter collected:

Aulacomnium androgynum	r.	Eurhynchium praelongum	
*A. palustre	o.	Hypnum cupressiforme	o.
*Brachythecium velutinum	r.	var. resupinatum	r.
Bryum erythrocarpum		*var. tectorum	
Ceratodon purpureus	o.	Tetraphis pellucida	
Dicranum scoparium	o.	Webera nutans	o.

Those marked with an asterisk were sometimes found on the smooth cut surfaces.

A certain number of lichens were also present. *Parmelia physodes* and *Cladonia pyxidata* sometimes occurred on the cut surfaces, but most of the lichens come in when the stumps are more decomposed. Other lichens besides those mentioned above are: *Cladonia silvatica* (r.), *C. furcata* (v.r.), *C. macilenta* (l.), *C. parasitica* (l.), *Lecanora varia* (o.), and *Lecidea uliginosa* (v.r.).

In some cases the stumps have gradually decayed away and merged into the surrounding soil, but in many cases a rather different state of affairs has come about. The inner portion of the stumps has either been burnt out or has decayed away leaving a small depression. In such places soil of a sort has collected and formed a suitable nidus for the establishment of higher plants. In 1924 the following were found in various stumps: *Epilobium angustifolium*, *Fagus silvatica* (seedling), *Ranunculus repens*, *Betula* (seedlings) and *Rubus* spp. In 1925 *Molinia caerulea*, *Sorbus aucuparia* and *Deschampsia flexuosa* were also seen, while *Epilobium* was relatively frequent in hollow or decayed stumps. In the November of 1924 it was noticed that the stumps were rapidly rotting away inside although often preserving a smooth and rigid outer shell. No doubt within a few years they will have almost completely disappeared.

4. SUMMARY AND CONCLUSIONS

1. The recolonisation of an area of felled sub-spontaneous pinewood is described.

2. The progress of colonisation and the communities formed are dealt with, it being shown that different lines of succession are followed on dry and wet areas.

3. On the former ordinary dry-heath communities of *Calluna* and *Pteridium* are being formed, while *Betula alba* and *B. pubescens*, in addition to forming pioneer communities themselves, are invading the other parts. The distribution and advance of *Epilobium angustifolium* are especially fully treated, while data as to powers of dispersal, etc. of other species are given.

4. On the wet regions the main dominant is *Molinia caerulea* which covers large stretches. *Juncus* spp. (especially *J. effusus* and *J. conglomeratus*) seem to be invading these *Molinia* communities. All the consocies on the damper parts are ahead of the drier types in development and are completely closed. Two factors are suggested to explain this: the presence of *Molinia* in the damp parts of the original wood and the more favourable soil conditions in these areas after felling.

5. Young trees of *Betula* spp. are to be found everywhere; it seems as though both wet and dry regions are being converted into a scrub, mainly of birches, and finally into woodland. The small part played by *Pinus* in the primary phases of the process is noteworthy, but the evidence suggests that eventually, on the damp areas at least, pinewood will be re-established.

6. The effect of fires on the felled region is described. In particular the disastrous fires of 1921 are dealt with, and it is shown that burning greatly alters the course of colonisation. The new successions initiated are followed in detail, the wet and dry regions agreeing in that *Funaria* and *Epilobium angustifolium* are the dominant plants in the earlier stages, while later on *Ceratodon* replaces *Funaria*; but after this the successions diverge, the usual dominants of the two regions, viz. *Calluna* on the dry areas and *Molinia* and *Juncus* spp. on the damp areas, becoming more abundant. *Betula* seedlings also appear at an early stage and this will probably result in a telescoping of some of the normal stages.

7. The special floras of ruderal areas and of the pine-stumps are described.

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STUDIES ON THE ECOLOGY OF ENGLISH HEATHS

III. ANIMAL COMMUNITIES OF THE FELLING AND BURN SUCCESSIONS AT OXSHOTT HEATH, SURREY

By O. W. RICHARDS.

(*With twenty-nine Tables and two Figures in the Text.*)

CONTENTS.

INTRODUCTION AND ACKNOWLEDGMENTS

Notes have already been published on the animals occurring on the unfelled and unburnt parts of Oxshott Heath (see this JOURNAL, **12**, 1924, pp. 291–2, 299–301, 304–5). The following account gives the results of a primary survey of the animals of the felled and burnt parts of the Common made in 1922–5. In such a survey identification of specimens is a large part of the work, and I have much pleasure in acknowledging assistance in identification given as follows: Coleoptera, Commander J. J. Walker and Mr J. Collins; Hymenoptera and Diptera, Mr A. H. Hamm; Micro-lepidoptera, Mr E. G. R. Waters; Aphides, Mr F. Laing; Spiders, Dr A. R. Jackson. Dr Jackson, in particular, has named every spider I have captured. Mr W. J. Lucas has also been kind enough to allow me to use some of his notes. Even with all this help, it will be seen that certain groups (e.g. parasitic Hymenoptera) have been more or less neglected.

In the lists given in the paper, the groups of animals are always arranged in the same way; within each group the genera are arranged alphabetically and it is hoped that this may allow those who are interested in some of the groups only to extract the information they require more easily.

This paper cannot pretend to give the same amount of information about the succession of animal communities after felling as has been given in the

case of the plants[1]. Animal ecology, however, has been so much neglected in England that it was thought that any information about the animals would be useful in an area where the plants had been studied and where the vegetational seres identified are easily recognised elsewhere, especially since the plants must in any case be studied first.

Although the succession of the animals has not been studied in detail, yet a certain amount of information on this subject has been obtained. Animal succession is probably of a different nature to plant succession. In the latter, as a general rule, dispersal mechanisms are good enough to allow all the candidates for a bare area to arrive fairly soon, and succession consists in the replacing of one dominant by another as the conditions become suitable for the various dominants. In the case of animals, however, where dominance does not exist, the species in a particular habitat tend to form communities attached to particular plants by a chain of food relations. In each case there are some small animals eating the plant and from that starting point there is a series of carnivores and parasites, the former of gradually increasing size. Such communities, of course, have many species in common and the largest carnivore, which may perhaps be a hawk, will be at the end of a large number of food chains leading to different plant associations.

Animal succession then comes to mean changing the food chain attached to one dominant into another attached to its successor. To show this change accurately, the alterations in a definite quadrat would have to be recorded; but in the case of the animals time was not available for such detailed work. It has, however, been found that when a new dominant arrives, most of the fauna attached arrives within a year or two, and that sometimes the change in the fauna may be very complete and rapid.

In many cases it has been found that the animal community has been slowly changing while the plant community has shown no comparable change. Thus during the colonisation of bare ground by *Calluna*, while *Calluna* spends several years in growing together to form a continuous carpet, the animal fauna is changing not only in its abundance but in its constituent species. The main factor responsible for this change is the gradual arrival of species with imperfect means of dispersal, though habitat changes may sometimes play a part as well. This lag in the occupation of suitable territory is, of course, shown in plants as well, but is probably rarely so marked as it is in animals. In the case of animals it becomes necessary as a consequence to make very careful comparative studies before the real causes of changes in the communities can be detected.

The final arrangement of animals in chains leading to particular plants requires much more knowledge of the food habits than exists at present. The data for Oxshott are very incomplete and most of the foods given for the animals are taken from text books rather than discovered by observations on

[1] See the immediately preceding paper in this issue, pp. 203–243.

the spot. This applies especially to the carnivores, the details of whose food habits are most in need of study.

It seems to be true that, as a general rule, animals are attached to plants by some sort of food relation rather than by the need of similar habitat conditions. No doubt many examples can be given of animals whose distribution is controlled by definite edaphic or physiological requirements, but probably these are usually the species which, though highly characteristic of an association, are not the most common animals in it. The commonest animals in a plant community are often those most common elsewhere. Thus, in this account, all the animals associated with a plant dominant are treated together, though the plant may be growing in what, from the point of view of plant ecology, are several habitats. An animal community may also occur in very small areas owing to the presence of the plant with which it is associated, and areas which botanically speaking are fairly homogeneous and represent a definite plant community may contain several fairly distinct animal communities.

The divisions used here are to a great extent those described and defined in "Studies on the Ecology of English Heaths," Parts I and II (this JOURNAL, **12**, 1924, p. 287 and **14**, 1926, p. 203), dealing with the plant ecology of the district.

1. DRY SERIES

A. BARE AREAS.

There are a number of animals that are characteristically found on bare sand. The most typical are the sand wasps, the fly *Anthrax*, and the tiger beetles, which often fly up as one walks across the Common. Normally such species inhabit paths, sandpits, etc., but at Oxshott there has been a great extension of their habitat. Few of the species live entirely on the bare areas, since most have to obtain their food from various plant communities, but many are controlled by the amount of bare sand available for nesting sites. A thick layer of humus usually makes a bare area unacceptable, so that for many species it is only the steeper slopes and the places where the humus has been burnt or blown away that are used. Since this community is merely an association of forms with similar nesting requirements, there is no regular food-cycle amongst its members. The species in Table I occur on dry, bare areas all over Oxshott Common, except in the pinewood which is too shady for most of them. Not enough data are available to determine the rates at which different species colonise new areas. The list of the bees and wasps includes only the most abundant species; it is hoped that this group will be more fully dealt with in a later paper.

Table I. *Animals of bare sand.*

	Species	*Food*	*Nesting place or other habitat*
Bee	Andrena argentata Sm.	Pollen and nectar (*Calluna*)	Nests in flat, hard sand
"	A. dorsata K.	" " (*Rubus, Epilobium*)	" " "
"	A. fulva Schr.	Pollen and nectar (*Salix*)	" " "
"	A. fuscipes K.	" " (*Calluna*)	" " "
"	A. gwynana K.	" " (*Salix*)	" " "
"	A. ovatula K. (afzeliella)	" " (*Rubus*)	" " "
"	A. sericea Schr.	" "	" " "
Digger wasp	Cerceris arenaria L.	Weevils	Nests in sandy slopes
"	C. labiata F.	"	" " "
"	C. rybyensis L.	Small bees	Nests in sandy cliffs
"	Ceropales maculata F.	A parasite of *Psammochares*	
Bee	Colletes succinctus L.	Pollen and nectar (*Calluna*)	Nests in flat sand especially paths
Digger wasp	Crossocerus wesmaeli Vid.L.	Flies	Nests in cliffs and slopes
"	Diodontus minutus F.	Aphides	Nests in sandy cliffs
"	Evagetes bicolor Lep.	Spiders	Nests in flat sand
Ant	Formica fusca L.	Insects and secretions of aphides	Nests mainly under pine bark
Digger wasp	Gorytes quadrifasciatus F.	Homoptera	Nests in flat sand, or humus
"	G. tumidus Pz.	"	?
Bee	Halictus flavipes F.	Pollen and nectar (*Calluna, Erica, Rubus*)	?
"	H. minutus Zett.	Pollen and nectar	Nests in sandy cliffs
"	H. morio F.	" "	" " "
"	H. prasinus Sm.	" " (*Calluna, Erica*)	Nests in flat sand
"	H. punctatissimus Sch.	Pollen and nectar (*Ulex, Rubus*)	?
"	H. rubicundus Chr.	Pollen and nectar (*Calluna, Rubus*)	Nests in flat sand
"	H. villosulus K.	Pollen and nectar (Yellow composites)	" "
Ruby wasp	Hedychridium minutum Lep.	Parasite of digger wasps	
Bee	Megachile circumcincta Lep.	Nectar and pollen (*Rubus*)	Nests in flat sand
"	M. maritima K.	" " (*Rubus* and *Lotus*)	" "
Digger wasp	Mellinus arvensis L.	Flies	Nests in flat sand (and cliffs)
"	Methoca ichneumonides Latr.	Parasite of tiger beetles	
"	Miscophus concolor Dahlb.	Small spiders	Nests in flat sand
"	Myrmosa melanocephala F.	Parasite of other aculeates	
Bee	Nomada rufipes F.	Parasite of *Andrena fuscipes*	
"	N. signata Pz.	Parasite of *A. fulva*	
Ruby wasp	Notozus panzeri F.	Parasite of *Psen*	
Digger wasp	Nysson dimidiatus Jur.	Probably parasite of *Gorytes tumidus*	
"	N. interruptus F.	Probably parasite of *G. quadrifasciatus*	
"	Oxybelus uniglumis L.	Flies	Nests in flat sand
"	Priocnemis parvulus Dahlb.	Spiders	Nests in flat sand (also humus)
"	Psammochares chalybeatus Schiodte	"	Nests in flat sand
"	Ps. fuscus L. (viaticus)	"	Nests in flat sand and slopes
"	Ps. nigerrimus Scop.	"	Nests in flat sand
"	Ps. pectinipes V.deLind.	Parasite of its congeners	
"	Ps. plumbeus F.	Spiders (esp. *Trochosa*)	Nests in flat sand and slopes
"	Ps. rufipes L.	"	Nests in flat sand
"	Psen shuckardi Wesm.	Homoptera	Nests in flat sand and cliffs

Table I (*continued*).

	Species	Food	Nesting place or other habitat
Bee	Saropoda bimaculata Pz.	Pollen and nectar (*Erica, Rubus, Epilobium*)	Nests in flat sand
,,	Sphecodes affinis v.Hag.	Parasite of Halictus	
,,	S. gibbus L.	,, ,,	
,,	S. divisus K. (similis)	,, ,,	
Digger wasp	Sphex (Ammophila) campestris Latr.	Caterpillars (birch)	Nests in flat sand
,,	S. (A.) sabulosa L.	,, (birch and *Calluna*)	,, ,,
,,	Tachysphex pectinipes L.	Grasshoppers	,, ,,
,,	T. unicolor Pz.	,,	,, ,,
		DIPTERA	
Fly	Anthrax fenestratus Fall.	Parasite of grasshoppers	Adult sits on bare ground
,,	Miltogramma punctatum Mg.	Parasite of *Colletes*	
,,	Paragus tibialis Fall.	? Perhaps a parasite	Associates with small aculeates
,,	Sciapus loewi Beck.	Larva subterranean and probably carnivorous	Adult often in rabbit holes
,,	Sphixapata conica Fall.	Parasite of *Mellinus* and probably of other digger wasps	
		LEPIDOPTERA	
Moth	Salebria fusca Hw.	Larva on *Erica*	On burnt areas
		COLEOPTERA	
Dung beetle	Aphodius tristis Pz.	Larva and adult on dung	? Associated with rabbits
Beetle	Bembidium lampros Hbst.	Carnivorous	
,,	Byrrhus fasciatus F.	?	Trapped in rabbit holes
Tiger beetle	Cicendela campestris L.	Carnivorous	
,,	C. silvatica L.	,,	
Dor beetle	Geotrupes pyrenaeus Charp.	Dung	Associated with rabbits
,,	G. typhoeus L.	,,	
Beetle	Metabletus forcola Gyll.	Carnivorous	
,,	Microzoum tibiale F.	?	
		HEMIPTERA	
Bug	Zicrona coerulea L.	? Carnivorous	Associated with burnt areas
		ORTHOPTERA	
Grasshopper	Tettix bipunctatus L.	Herbs	Flat places, mostly damper parts
		ACARINA	
Mite	Erythraeus regalis C.L.K.	? Carnivorous	
		ARACHNIDA	
Spider	Aelurillus insignitus Cl.	Carnivorous	
,,	Lycosa lugubris Walck.	,,	
,,	L. monticola C.L.K.	,,	
,,	L. nigriceps Thor.	,,	
,,	L. pullata Clerck.	,,	
,,	L. tarsalis Thor.	,,	
,,	Tarentula barpipes Sund.	,,	
,,	Trochosa picta Hahn.	,,	Lives in burrows in the sand
		OPIOLIONIDA	
Harvestman	Oligolophus tridens	Carnivorous	
,,	Mitopus morio F.	,,	
		MAMMALIA	
Rabbit	Oryctolagus cuniculus L.	Short plants	Mainly burrows in bare areas. Penetrates the pinewood with its dung beetles

B. CALLUNETUM.

The animal community associated with *Calluna* is a very definite one, and seems to be mainly controlled by the plant rather than by any special edaphic or physiological conditions. Thus the fauna of *Calluna* in woods, in damp places, and in dry, burnt or unburnt areas, is very similar, particularly as regards the most abundant species. *Erica cinerea* and *E. tetralix* seem also to support practically the same set of animals, but probably more accurate observations would show differences. The description of the animal community associated with *Calluna* at Oxshott presents certain difficulties which are met with to some extent in the study of all the communities on the Common. The older, more or less permanent areas of Callunetum have been much interfered with by man and many typical animals are rare or absent. Many of these, however, occur in the now extensive new areas of *Calluna*, and the list in Table II is made by combining the records. Obviously there is a great danger of recording as Callunetum animals those which really only occur in the early stages of colonisation. Probably further study, especially in other districts, would show which species were primarily pioneers. Many species have been found only in the older Calluneta and these may be absent from the newer areas for a number of reasons. First it is very difficult to be certain that the observations have been complete enough; many forms are difficult to find even when common, and many only occur as adults during a short part of the year. There are, however, two factors which are universally important, namely, the effect of the varying powers of dispersal and of different edaphic needs.

(1) *Dispersal.* A number of *Calluna* insects are unable to fly (usually owing to secondary loss of wings) and these do not occur as a rule in early stages of colonisation. The beetles *Helops striatus* Fourc. and *Carabus catenulatus* Scop. are exceptions. Both are wingless, yet the former is always one of the earliest arrivals on a burnt area. The *Carabus* is well known to walk about a lot in the night and owing to its large size covers the ground quickly. The following wingless insects only occur in the older Callunetum including isolated patches in the felled area which escaped burning and represent slight openings in the old pinewood: the beetles *Othius myrmecophilus* Kies., *Strophosomus coryli* F., *S. lateralis* Pk.; and the Leaf hopper *Ulopa reticulata* F. The last two species are common on most heaths, feeding on *Calluna*. Other forms are probably too small to fly far, except under favourable circumstances, e.g. the beetle *Hypocyptus longicornis* Pk. and the fly *Limosina* spp. Where trees were growing before the fire a few species escaped by crawling up the trees. Probably this was the case with the woodlouse *Philoscia muscorum* Scop. which occurs under *Calluna* in the older areas and also under bark of burnt chestnut in parts of the Molinietum. In the same way escaped the larvae of a wingless moth, *Luffia ferchaultella* Stph. which fed on the lichens on the trunks.

(2) *Edaphic conditions*. There are many other species which are only found on older Calluneta but for whose distribution no definite reason can be given. These species are given in Table III. The newer areas lack the dense, moist moss carpet that is found in well developed Calluneta and this must have an important effect on many species. Thus the mollusc *Polita radiatula* Alder only occurs in the moss, and beneath it the slugs lay their eggs. When *Betula* grows up its leaves form an equally good cover for slugs' eggs.

In woods near Oxford many of the larger Staphylinid beetles (*Ocypus*, *Quedius*, *Philonthas*) are commonly found hibernating under moss in winter, often in very large numbers. Such beetles only occur at Oxshott on the Calluneta with moss, and this may be the controlling factor. Other insects, e.g. larvae of Syrphid flies and sawflies pupate under moss and might be similarly controlled. The species of spiders have very good powers of dispersal so that anomalies in their distribution ought mainly to be due to edaphic conditions. It will be seen that in the genera *Leptyphantes*, *Centromerus* and *Walchenaera* some species have not been found on the new areas, and these may be controlled by the edaphic conditions.

The beetles of the genus *Bradycellus* have a curious distribution. An isolated specimen of *B. verbasci* Duft. was found in the Molinietum. The Callunetum species are *B. harpalinus* Dj. and *B. similis* Dj. The former is mainly a pioneer which disappears or becomes rare in the later stages, while the latter is not uncommon in any Callunetum but does not colonise quickly. The following are the data for the two species.

In the old heather on the south ridge *B. harpalinus* is rare, while *B. similis* is often common, especially in winter. In the new areas in 1922 and 1923 (i.e. for two years after the fire) only *B. harpalinus* occurred, and it was very abundant under *Calluna*. It also occurred commonly under charred pine bark, where *B. similis* is never found. The isolated relict areas of *Calluna* probably contained *B. similis* in 1922–3, and in early 1924 *B. similis* was the commoner of the two there. On these areas their numbers are now about equal. In like manner *B. similis* appeared under the new *Calluna* in 1924 and seems now to have become the commoner species. Under *Calluna* on the damper areas *B. similis* seemed to arrive earlier. Apparently *B. harpalinus* is the best coloniser (both have well developed wings) while *B. similis* needs the damper conditions which, when the moss carpet is continuous, drive out *B. harpalinus*.

The detailed changes which result from a colonisation by *Betula* have not been recorded. There is certainly a stage when the two communities are present in alternating patches. A few notes have been made on the effect of *Betula* leaves on the *Calluna* fauna. Certain forms, e.g. *Stenus geniculatus* Gr. and *Amphigynus piceus* Marsh, are normal inhabitants of *Calluna* in the early stages of invasion. The latter beetle has not been found at Oxshott, perhaps because it is wingless, but it occurs on other London heaths. The dead leaves

also favour mollusca, allowing them to lay their eggs in a damp situation. Some of the birch-feeding larvae may be found pupating under neighbouring *Calluna* bushes. Probably most of the birds seen on the new *Calluna* areas really nest in the invading birches. A moth, *Acidalia interjectaria* B., also seems to be characteristic of the scrub stage of invasion, especially in hollows.

The general habitat of most of the *Calluna* animals is on the ground beneath the bushes of heather. Nearly all moths hide in the bushes by day and can be beaten out. The exact habitats of the species in this list will therefore not always be given. There is a separate list of the flower visitors to *Calluna*, and to the species of *Erica*. Except when the heather is in flower, the animals are not at all conspicuous; nearly all the small forms, which hide under heather, are not conspicuous even when abundant.

Table II. *Animal community of typical Callunetum (except forms only found on long established areas).*

	Species	*Food*	*Habitat*
		HYMENOPTERA	
Wasp	Eumenes coarctata L.	Feeds larva on caterpillars	Makes a mud nest on heather
Ant	Formica fusca L.	Insects and secretions of aphides	Nests mainly under pine bark
Digger wasp	Miscophus concolor Dahlb.	Heath spiders (*Stemonyphantes*)	Nests in bare sand
Ant	Myrmica ruginodis Nyl.	Insects and secretions of aphides	Nests under *Calluna* or pine bark. Especially damper parts
,,	M. scabrinodis Nyl.	Insects and secretions of aphides	As above but in dry places
,,	M. sulcinodis Nyl.	Insects and secretions of aphides	Nests under pine bark in dry places
Wasp	Vespa vulgaris L.	Heather insects	Nests in scrub and wood areas
		DIPTERA	
Fly	Aphiochaeta pulicaria Fall.	Larva a scavenger	
,,	A. mallochi Wood	,,	
,,	Chaetoneurophora curvinervis Beck	Larva on carrion	The species may be associated with rabbits
,,	Cryptolucilia caesarion Mg.	Larva a scavenger	Adult under heather in winter
,,	Enoplopteryx ciliatocosta Ztt.	Larva carnivorous	Adult under heather in winter
,,	Euaresta conjuncta Lw.	Larva on some undetermined plant	Adult under heather in winter
,,	Gonia ornata Mg.	Parasite of *Agrotis*	Adult flies in early spring
,,	Machimus atricapillus Fall.	Larva and adult carnivorous	
,,	Oscinis spp.	Larva on grasses	Adult under *Calluna* in winter
,,	Phaonia signata Mg.	Larva ? scavenger	Adult under *Calluna* in winter
,,	Scatella stagnalis Fall.	?	
,,	Scatophaga stercoraria L.	Larva ? scavenger	Adult carnivorous mainly in summer
,,	Sciara sp.	,, ,,	Adult under *Calluna*
,,	Sepsis, at least 2 spp.	,, ,,	,, ,,
Hover fly	Sphaerophoria scripta L.	Larva on aphides	Adult on flowers
Crane fly	Tipula spp.	Larva subterranean	
Fly	Wagneria lugens Mg.	Parasite of noctuid caterpillars	Adult runs about on bare ground in Sept.

Table II (*continued*)

	Species	*Food*	*Habitat*
		LEPIDOPTERA	
Moth	Acidalia straminata Tr.	Larva on herbs	Adult hides in *Calluna*
,,	Agrotis pronuba L.	,,	Adult visits *Calluna*
,,	A. tritici L.	,,	Flies in early spring
,,	Amphisbatis incongruella Stt.	Larva on *Calluna*	Adult visits *Calluna* flowers
,,	Anarta myrtilli L.	,,	
,,	Aristotelia ericinella Dup.	,,	
,,	Coleophora juncicolella Stt.	,,	
,,	Crambus culmellus L.	Larva on grasses	Perhaps only a pioneer
,,	C. geniculeus Hw.	,,	,, ,, ,,
,,	Ematurga atomaria L.	Larva on *Erica* and Leguminosae	
,,	Eupithicia nanata Hb.	Larva on *Calluna* and *Erica*	
,,	Gelechia affinis Dgl.	Larva on mosses	Adult hides in *Calluna*
,,	G. ericetella Hb.	Larva on *Calluna* and *Erica*	
,,	G. umbrosella Z.	Larva ? on mosses	Adult hides in *Calluna*
,,	Lasiocampa quercus L.	Larva on *Calluna* and various trees	
,,	Phoxopteryx (Ancylis) uncana Hb.	Larva on *Erica* and birch	Commoner on damp parts
,,	Pleurota bicostella Cl.	Larva on *Erica*	
,,	Plusia gamma L.	Larva on herbs	
,,	Plutella maculipennis Curt.	,,	
,,	Pterophorus monodactylus L.	,,	Hibernates in *Calluna*
,,	Salebria fusca Hw.	Larva on *Erica*	
,,	S. palumbella F.	Larva on *Calluna*	
,,	Scythris grandipennis Hw.	Larva on *Ulex*	
,,	S. variella Stph.	Larva on *Calluna* and *Erica*	Adult hops about on bare ground
		COLEOPTERA	
Beetle	Amara famelica Zimm.	Carnivorous	Perhaps only a pioneer
,,	A. familiaris Duft.	,,	Especially damper parts
,,	Anthicus antherinus L.	Scavenger	
,,	Bradycellus harpalinus Dj.	Carnivorous	Newer areas
,,	B. similis Dj.	,,	Older areas
,,	Calathus melanocephalus L.	,,	Perhaps more abundant where birch invades
,,	Carabus catenulatus Scop.	Carnivorous (worms and snails)	
,,	Coccinella 7-punctata L.	Aphides, etc.	
,,	C. 11-punctata L.	,,	
,,	Cryptocephalus fulvus Goez.	*Rumex acetosella*	Adult hibernates under *Calluna*
,,	Helops striatus Fourc.	Larva carnivorous under *Calluna*	Adult in nearly all habitats
,,	Metabletus foveola Gyll	Carnivorous	
,,	Mycetoporus splendens Marsh	,,	Perhaps where birch invades
,,	Notiophilus biguttatus F.	,,	Especially in wet places
,,	Olisthopus rotundatus Ph.	,,	Does not arrive for two years
,,	Quedius boops Gr.	,,	
,,	Simplocaria semistriata F.	?	
,,	Stenus atratulus Er.	Carnivorous	Damper places
,,	S. geniculatus Gr.	,,	When *Betula* invades
,,	S. rogeri Kr.	,,	Damper places
,,	Tachyporus chrysomelinus L.	Carnivorous	
,,	T. hypnorum F.	,,	
,,	Xantholinus linearis Ol.	,,	
		HEMIPTERA	
Bug	Coranus subapterus	Carnivorous	
,,	Cymus melanocephalus Fieb.	?	

Table II (*continued*).

	Species	Food	Habitat
		HEMIPTERA	
Bug	Macrodema micropterum Curt.	?	
,,	Nabis ericetorum Schltz.	Carnivorous	
,,	Orthotylus ericetorum Fall.	*Calluna* and *Erica*	
,,	Scolopostethus decoratus Hhn.	?	
,,	Trapezonotus arenarius L.	?	
,,	Triphleps nigra Wolff.	? Carnivorous	
Leafhopper	Acocephalus albifrons L.	? *Calluna*	
Psyllid	Rhinocola ericae Curt.	*Calluna* and *Erica*	
Mealy wing	Aleyrodid ? sp.	Vegetarian	Very abundant under *Calluna*
		COLLEMBOLA	
Springtails	Collembola (unidentified)	Very abundant, vegetarian	
		THYSAMIRA	
	Campodea sp.	Vegetarian	
		ORTHOPTERA	
Grasshopper	Gomphocerus maculatus Thunbg.	Herbs	
,,	Metrioptera brachyptera L.	,,	Mainly damper places
,,	Tettix bipunctatus L.	,,	
		ARACHNIDA	
Spider	Centromerus concinnus Thor.	Carnivorous	
,,	Leptyphantes tenuis Bl.	,,	
,,	Mangora acalypha Walck.	,,	Damper places
,,	Pisaura mirabilis Clerch.	,,	
,,	Stemonyphantes lineatus L.	,,	
,,	Tarentula barbipes Sund.	,,	
,,	Walckenaera nudipalpis Westr.	,,	Damper places
,,	Wideria antica Wid.	,,	
,,	Xysticus cristatus Clerck.	,,	
		OPILIONIDA	
Harvestman	Phalangium opilio L.	Carnivorous	
		ACARINA	
Mite	Erythraeus regalis C.L.K.	Carnivorous	Under *Calluna* and on bare soil
		CRUSTACEA	
Woodlouse	Porcellio scaber Latr.	Scavenger and carnivorous	Newer areas
		CHILOGNATHA	
Centipedes		Carnivorous	
		DIPLOPODA	
Millipedes		? Scavengers	
		ANNELIDA	
Earthworm		Vegetarian	Damper parts of felled areas
		REPTILIA	
Grass snake	Tropidonotus natrix L.	Carnivorous	Damper parts
		AVES	
Yellow Hammer	Emberiza citrinella citrinella L.	Chiefly plants	
Partridge	Perdix perdix perdix L.	Chiefly plants, insects more in summer	
Stonechat	Saxicola torquata hibernans Hart.	Mainly insects	
		MAMMALIA	
Rabbit	Oryctolagus cuniculus L.	Herbs and Ericaceae	

Table III. *Species found only on older Callunetum.*

1 = Older *Calluna*. 2 = Pinewood, *Calluna* and *E. tetralix*. 3 = Relict *Calluna* in felled areas.

Ant	Acanthomyops alienus Först. 1	Insects and secretions of aphides	Nests in sand
,,	A. umbratus Nyl. 1	Insects and secretions of aphides	Nests under *Calluna* and moss
,,	Myrmica lobicornis Nyl. 1, 3	Insects and secretions of aphides	Nests under *Calluna*
		LEPIDOPTERA	
Butterfly	Lycaena aegon Schiff. 1	Larva on *Erica* and *Ornithopus*	Abundant on older *Calluna*
		DIPTERA	
Fly	Limosina luteilabris Rdi. 1, 2	? Scavenger	Adults under moss
,,	Sphaerocera subsaltans F. 1	,,	
		COLEOPTERA	
Beetle	Amara lunicollis Schiod. 1, 3	Carnivorous	
,,	A. trivialis Gyll. 1	,,	
,,	Astilbus canaliculatus F. 1	Ants	
Ladybird	Chilocorus similis Ross. 1	? Aphides	
Beetle	Hypocyptus longicornis Pk. 2, 3	? Scavenger	? Too small to fly far
,,	Lochmaea suturalis Th. 1, 2	*Calluna* and *Erica*	
,,	Nebria brevicollis F. 2, 3	Carnivorous	
,,	Ocypus cupreus Ross. 1	,,	
,,	O. olens Müll. 1	,,	
,,	Othius myrmecophilus Kies. 2 (3?)	?	Wingless
,,	Philonthus marginatus F. 1	Carnivorous	
,,	P. politus F. 1	,,	
,,	Quedius molochinus Gr. 3	,,	
,,	Q. nigriceps Kr. 2	,,	
,,	Sipalia circellaris Gr. 1, 2	? Carnivorous	
,,	Strophosomus coryli F. 1, 2, 3	Vegetarian	Wingless
,,	S. lateralis Pk. 1, 2, 3	*Calluna* and *Erica*	,,
		HEMIPTERA	
Leafhopper	Dicraneura variata Hardy 1	Vegetarian	
,,	Ulopa reticulata F. 1, 2, 3	*Calluna*	Wingless
		ORTHOPTERA	
Cockroach	Ectobius lapponicus L. 1, 3	? Scavenger	Short-winge
Grasshopper	Stauroderus bicolor Charp. 1, 3	Vegetarian	
		ARACHNIDA	
Spider	Agroeca proxima Cambr. 1	Carnivorous	
,,	Centromerus bicolor Bl. 1, 3	,,	
,,	C. silvaticus Bl. 1	,,	
,,	Cheiracanthium carnifex F. 1, 3	,,	
,,	Dictynna arundinacea L. 3	,,	
,,	Leptyphantes ericaeus Bl. 3	,,	
,,	Linyphia pusilla Sund. 3	,,	
,,	Micryphantes rurestris C.L.K. 1	,,	
,,	Nematognus obscurus Bl. 1	,,	
,,	Robertus lividus Bl. 1	,,	
,,	Walckenaera acuminata Bl. 1, 3	,,	
		OPILIONIDA	
Harvestman	Nemastomum lugubre Bl. 2	Carnivorous	
,,	Oligolophus agrestis. 2	,,	
,,	Platybunus corniger Fr. 2	,,	
		CRUSTACEA	
Woodlouse	Philoscia muscorum Scop. 1, 2	? Scavenger and carnivore	
		MOLLUSCA	
Slug	Eggs under moss. 1, 2	Vegetarian and scavenger	
Snail	Polita alliaria Müll. 2	,, ,,	
,,	P. radiatula Alder. 1	,, ,,	

Table IV. *Insect visitors of* Calluna *and* Erica *flowers.*

Ca. = *Calluna*. Ci. = *Erica cinerea*. T. = *E. tetralix*. W. = Worker. F. = Female. M. = Male.

		Hymenoptera	
Bee	Andrena argentata Sm.	F. Ca.	Cf. Table I
,,	A. fuscipes K.	F. Ca.	,,
Hive Bee	Apis mellifera L.	W. Ca. Ci.	From surrounding houses. Very common
Humble Bee	Bombus agrorum F.	W. Ca. Ci. W. F. T.	The commonest one on T.
,,	B. hortorum L.	W. T.	
,,	B. jonellus K.	W. Ca. W. M. Ci. W. F. T.	
,,	B. lapidarius L.	M. Ca. M. W. F. Ci. W. T.	The commonest one on Ci.
,,	B. lucorum L.	M. Ca. M. W. F. Ci. W. T.	Very common on Ci.: the W. bites through the corolla at least of T.
,,	B. ruderarius Müll. (derhamellus K.)	M. W. T.	
,,	B. sylvarum L.	F. T.	
,,	B. terrestris L.	M. W. Ca. M. Ci. W. T.	Sometimes bites through corolla but not seen to do so here
Bee	Colletes succinctus L.	F. M. Ca.	Cf. Table I. An abundant *Calluna* bee.
,,	Halictus flavipes F.	M. Ca. F. Ci.	Cf. Table I
,,	H. minutus Zett.	M. F. Ca.	,,
,,	H. prasinus Smith	F. Ci.	,,
,,	H. punctatissimus Sch.	F. Ci.	,,
,,	H. rubicundus Chr.	M. Ca. T.	,,
,,	Megachile maritima K.	M. Ci.	,,
,,	M. willughbiella K.	M. Ci.	Cf. Table XXIX
,,	Nomada rufipes F.	M. Ca.	Cf. Table I
,,	Prosopis genalis Th.	F. Ci.	Cf. Table XXIX
,,	Saropoda bimaculata Pz.	M. F. Ci.	Cf. Table I
Digger wasp	Sphex (Ammophila) sabulosus L.	M. Ca. Ci.	,,
		Diptera	
Fly	Conops quadrifasciatus DeG.	Ca.	? Parasite of Humble Bees
,,	Volucella bombylans L.	F. Ca. T.	Commensal of Humble Bees
		Lepidoptera	
Moth	Agrotis tritici L.	Ca.	Cf. Table II
,,	Anarta myrtilli L.	Ca. Ci.	,,
,,	Plusia gamma L.	Ca. Ci.	,,

C. *Epilobium angustifolium.*

A small animal community is associated with this plant wherever it grows at Oxshott; in other places where the plant is more permanent (e.g. cut down woods near Oxford) there are rather more kinds of insects attached to it.

Only one moth feeds on *Epilobium* at Oxshott, *Mompha raschkiella* Z. A single specimen was found in 1923. In 1924 it was common amongst particular patches of the plant, and in 1925 it was common throughout and locally abundant. The adult appears in July. The most important enemy of the willowherb, however, is a beetle, *Haltica oleracea* L. Two specimens were found in July 1924 in the Great Hollow. In the winter of 1924–5 the adults were found hibernating in great abundance in *Polytrichum* and *Molinia*

tufts in the damp areas. In late June 1925 the larvae were a plague on the leaves of *Epilobium*. The larva feeds on the underside and the lower leaves are attacked first. Short or young plants may be killed off, all the leaves being destroyed. On the area invaded by *Calluna*, where *Epilobium* grows to some extent in local clumps in small hollows, almost every clump was infected and at least three-quarters of the plants in each clump.

In the summer of 1924 a few plants in the Molinietum had the upper part of the flowering spike covered with a black aphid (not yet identified). This destroys the upper buds while the lower ones are in flower. Food is solicited from this aphid by the ant *Formica fusca* L. and it is eaten by the ladybirds (larva and adult) *Coccinella 7-punctata* L. and *Adalia bipunctata* L. and probably also by Syrphid larvae. The buds are also destroyed by the gall midge *Perrisia epilobii* F.Loew. which makes the buds swell up and fail to flower. These galls were common on 27. IX. 25. A spider, *Erigone dentipalpis* Wid., has been found to spin its web on *Epilobium*.

Table V. *Insect visitors of* Epilobium.

Bee	Andrena dorsata K.	Male. Cf. Table I
,,	Apis mellifera L.	Worker: by far the most important visitor
,,	Bombus agrorum F.	Workers
,,	B. lapidarius L.	Workers
,,	B. lucorum L.	Male and female
,,	B. pratorum L.	Males. Only in shrub areas on the S.E. side
,,	B. terrestris L.	Male and worker
Digger wasp	Cerceris arenaria L.	Male. Cf. Table I
,,	C. labiata F.	,, ,,
Bee	Cilissa leporina Pz.	Male
,,	Coelioxys rufescens Lep.	Female. Parasite of *Megachile*
,,	Halictus flavipes F.	Male. Cf. Table I
Ruby wasp	Hedychridium minutum Lep.	Cf. Table I
,,	Notozus panzeri F.	Male. Cf. Table I
Digger wasp	Psen bicolor F.	
,,	P. unicolor V.deL.	Cf. Table XXIX
Bee	Psithyrus quadricolor Lep.	Parasite of *B. pratorum* L. and found in the same situation
,,	Saropoda bimaculata Pz.	Male and female common
,,	Sphecodes divisus (similis) K.	Female. Cf. Table I
	DIPTERA	
Fly	Catabomba pyrastri L.	
,,	Sicus ferrugineus L.	
	COLEOPTERA	
Beetle	Adalia bipunctata L.	
,,	Coccinella 11-punctata L.	
	HEMIPTERA	
Bug	Plagiognathus arbustorum F.	
,,	Triphleps nigra Wolff.	Cf. Table II

D. DECIDUOUS WOODS.

In the previous paper on Oxshott (this JOURNAL, 1924, p. 304) a few moths were recorded from the mixed deciduous wood on the eastern boundary of the felled area. This community has since been much more fully studied. The most important trees for insects are *Betula* spp., *Quercus*, *Alnus* and *Castanea*. All these have invaded the felled areas to a certain extent, though in this respect *Betula* is much the more important. *Castanea*, even when

common, has very few insects specially attached to it in England. The data are not sufficient to show the details of the colonisation of young birches by animals, so the following plan has been adopted. A special table is given of species found on four-year-old birches (6–12 ft. high) on 22. VI. 25. Fairly extensive records were made on this date, and no difference could be detected between birches growing in different plant habitats. Many of the species in this table are commonly recorded from young birches by other observers, but this may be because animals are easier to see on trees that are not too tall; no doubt, however, some are real pioneers. A second table will be given of species found on Oxshott Common connected with deciduous trees or the undergrowth of the woods they form. Lengthy as this list is, it can only contain a fraction of the species that really occur. In particular the ground fauna has hardly been examined. The insects have been found in the main in two ways. Firstly, they may be found sitting on the palings in the mixed wood. This, especially in the case of moths, gives a sort of random sample of the population of such a wood, though certain genera are never found. Secondly, by beating young birches, oaks, etc., on the felled areas. Many of the species may be found whichever method of search is employed and it is not yet possible to distinguish those that are especially pioneers. The insect visitors of certain plants, such as *Rubus* (Table XIV) or *Teucrium scorodonia* (Table XI), which are specially common in birch scrub, are given separately. Certain animals are definitely associated with older birch woods, mostly species needing tree trunks for some part of their life history. Three lists are given: Trunk feeders, shown in Table VII by a symbol; Table VIII, inhabitants of *Polyporus betulinus* which only grows on the older trees; Table IX, animals living under bark. This last habitat was greatly extended when many birches were killed by fire in 1921. *Castanea* suffered in the same way, and the bark-fauna of the two trees is given in one list.

A few remarks have already been made on the effect of birch leaves on the *Calluna* fauna. In the case of the invasion of *Molinia* the inadequate data available are given in Table X. The most important effect is that wood-mice, almost certainly *Apodemus silvaticus* (none caught), become very abundant. Mollusca become common and lay their eggs, and birch feeding insects pupate under *Molinia* tufts more or less covered with birch leaves.

Table VI. *Insects on young* Betula. 22. VI. 25.

HYMENOPTERA

Sawfly	Croesus latipes Vill.	Larva found
Ant	Formica fusca L.	Attending aphides
Digger wasp	Psen shuckardi Wesm.	Hunting for Homoptera
Sawfly	Rhogogastera vividis L.	? Food
,,	Two unidentified larvae	Feeding on birch
Parasitic wasps	Braconids and Ichneumonids (e.g. Hemiteles spp.)	Abundant

Table VI (*continued*).

	DIPTERA	
Fly	Chelipoda melanocephala F.	Carnivorous. Common on underside of leaves
,,	Chilosia pagana Mg.	?
,,	Contarina betulina Kieff.	Galls common. Some with a parasite (Hym.)
,,	Empis livida L.	Carnivorous. Rare
,,	Gymnopternus aerosus Fall.	,, ,,
,,	Hilara interstincta Fall.	,, ,,
,,	Microchrysa polita L.	?
,,	Muscid flies of several kinds	Abundant
,,	Phalacrotophora fasciata Fall.	Parasite of *Adalia bipunctata*
,,	Tachydromia minuta Mg.	Carnivorous. Common
,,	T. flavipes F. ?	,, ,,
	LEPIDOPTERA	
Moth	Cacoecia unifasciana Dup.	Deciduous trees (incl. birch)
,,	Coleophora fuscedinella Z.	Larva on birch
,,	Drepana lacertinaria L.	Larva found
,,	D. falcataria L.	,,
,,	Eriocrania spp.	Blotches in leaves very abundant
,,	Olethreutes betulaetana Hw.	Rare. Larva on birch
,,	Orgyia antiqua L.	Larva common on birch, etc.
,,	Phylloporia bistrigella Hw.	Rare. Larva on birch
,,	Three or four species of unidentified larvae	
	COLEOPTERA	
Beetle	Adalia bipunctata L.	Very abundant. Mostly as larvae. Parasitised by Phalacrotophora
,,	Deporaus betulae L.	Common. Birch feeder
,,	Luperus rufipes Scop.	Abundant. Birch feeder
,,	Malthinus punctatus F.	Carnivorous. Common
,,	Orchestes rusci Hbst.	Rare. Birch feeder
,,	Phyllobius maculicornis Germ.	Common. Birch feeder
,,	Rhamphus flavicornis Clair.	Abundant. Birch feeder
,,	Rhynchites harwoodi Joy.	Common. Birch feeder
,,	R. nanus Pk.	Abundant. Birch feeder
,,	Strophosomus coryli F.	Common. Birch feeder
	HEMIPTERA	
Bug	Psallus betuleti Fall.	Common. Birch feeder
Aphides	Unidentified, but very abundant	,, ,,
Leafhopper	Empoasca smaragdula Fall.	Abundant. Birch feeder
,,	Oncopsis flavicollis L.	,, ,,
,,	O. rufusculus Fieb.	Common. Birch feeder
,,	Typhlocyba sp.	Abundant. Birch feeder

Table VII. *Deciduous wood community.*

Most of the Species recorded in Table VI are not repeated here.
* = Species characteristic of older woods
§ = Species lasting into the pinewood

	HYMENOPTERA	
Digger wasp	Cerceris arenaria L.	Preys on weevils on oak and birch. Cf. Table I
Sawfly	Croesus septentrionalis L.	Larva on deciduous trees, e.g. birch
Parasitic wasp	Exochilum brevicorne Gr.	Parasite of caterpillars
Sawfly	Fenusa pygmaea Kl.	Larva mines birch leaves (young birches)
Digger wasp	Mellinus arvensis L.	Hunts for flies. Cf. Table I
Sawfly	Monophadnus albipes Gmel.	Larva on birch (young birches)*
,,	Paururus noctilio F.	Larva on birch (wood)
Digger wasp	Passaloecus insignis V.deL.	Hunts for aphids on oak and birch
,,	Psen unicolor V.deL.	Hunts for Homoptera. Cf. Table
Sawfly	Scolioneura betuleti Klug.	Larva on birch (young birches)
Wasp	Vespa germanica Fab.	Nesting. Carnivorous §
,,	V. vulgaris L.	,, ,, §

Table VII (*continued*).

	DIPTERA	
Fly	Chrysopilus cristatus F.	Larva carnivorous and subterranean
,,	Dioctria atricapilla Mg.	Carnivorous
,,	D. hyalipennis F. (flavipes)	,,
,,	Hylos culiciformis F.	,,
,,	H. femoratus Mull.	,,
,,	Mesembrina meridiana L.	Scavenger
,,	Medeterus truncorum Mg.	Carnivorous on trunks*§
,,	Oedalea holmgreni Ztt.	Carnivorous
,,	Pipunculus zonatus Zett.	Parasite of Homoptera
,,	Platycnema pulicaria Fall.	?
,,	Sciapus platypterus Lw.	? Carnivorous
,,	Sphaerophoria scripta L.	Larva on aphides
,,	Syrphus torvus O.S.	,, ,, §
,,	S. tricinctus Fall.	,, ,,
,,	Volucella pelluceus L.	Commensal of wasps
	LEPIDOPTERA	
Moth	Acalla ferrugana Tr.	Larva on birch, abundant in rolled leaves of young birches. Autumn 1925
,,	Acidalia aversata L.	Larva on herbs§
,,	Acronycta psi L.	Larva on deciduous trees. Pupa under chestnut bark
Butterfly	Adopaea sylvanus Esp.	Larva on grasses. Adult on flowers, e.g. *Rubus*
Moth	Agrotis pronuba L.	Larva on herbs
,,	Aplecta nebulosa Esp.	Larva on deciduous trees
,,	Argyresthia brockeella	Larva on alder
,,	A. geodartella L.	Larva on alder and birch§
,,	A. glaucinella Z.	Larva on oak bark
,,	A. retinella Z.	Larva on birch§
,,	Boarmia consortaria F.	Larva on oak
,,	B. gemmaria Brahm.	Larva on deciduous trees§
,,	Borkhausenia lunaris Hw.	Larva on decayed wood
,,	Cacoecia lecheana L.	Larva on deciduous trees
,,	C. xylosteana L.	,, ,,
,,	Cabera pusaria L.	,, ,, §
,,	Camptogramma bilineata L.	Larva on herbs
,,	Capua angustiorana Hw.	Larva on deciduous trees
,,	Carcina quercana F.	Larva on oak
,,	Chimabache fagella F.	Larva on deciduous trees
Butterfly	Celastrina argiolus L.	Larva on holly and ivy
Moth	Coleophora bicolorella Stt.?	Larva on birch and alder (young birches)
,,	C. lutipennella Z.	Larva on oak
,,	Crambus pinellus L.	Larva on ? grasses
,,	Elachista cygnipennella Hb.	Larva on grasses
,,	Endotricha flammealis Schiff.	Larva on dead leaves
,,	Epiblema bilunana Hw.	Larva on birch catkins§
,,	E. similana Hb.	Larva on birch (young birches)
,,	E. solandriana L.	Larva on alder
,,	Eriocrania sp. undescribed	Larva on birch (young birches 3–4 years)
,,	E. purpurella Hw.	,, ,, ,,
,,	E. salopiella Stt.	,, ,, ,,
,,	E. senipurpurella Stph.	,, ,, ,,
,,	E. unimaculella Zett.	,, ,, ,,
,,	Euchloris pustulata Hufn.	Larva on oak
,,	Euchoeca obliterata Hufn.	Larva on alder
,,	Eupoecilia nana Hw.	Larva in catkins of birch
,,	Fumea casta Pall.	Larva feeds on refuse, pupates on trunks*§
,,	Gelechia luculella Hb.	Larva on oak
,,	G. proximella Hb.	Larva on birch
,,	G. umbrosella Z.	Larva on mosses
,,	Geometra papilionaria L.	Larva on deciduous trees
Butterfly	Gonepteryx rhamni L.	Larva on Rhamnus
Moth	Gracilaria alchimiella Sa.	Larva on oak
,,	Grapholitha ramella L.	Larva on birch (young birches)
,,	G. trimaculana Don.	Larva on elm

Table VII (*continued*).

	LEPIDOPTERA	
Moth	Hedya dealbana Fröl.	Larva on sycamore
,,	H. ocellana F.	Larva on deciduous trees
,,	Heliozele betulae Stt.	Larva on birch (young birches)
,,	Incurvaria muscalella F.	Larva on Rosaceae
,,	I. pectinea Hw.	Larva on birch (young birches)
,,	Larentia viridaria F.	Larva on galiun
,,	Lithocolletis faginella Z.	Larva on beech
,,	L. messaniella Z.	Larva on oak
,,	L. quercifoliella Z.	,,
,,	L. ulmifoliella Hb.	Larva on birch (young birches)
,,	Luffia ferchaultella Steph.	Larva on Lecanora varia, etc., on trunks*§
,,	Lyonetia clerckella L.	Larva on deciduous trees
,,	Monopis feruginella Hb.	?
,,	Notocelia uddmanniana L.	Larva on *Rubus*
,,	Oleuthreutes corticana Hb.	Larva on birch
,,	O. lacunana Dup.	Larva on *Rubus*, etc.
,,	Ornix betulae Stt.	Larva on birch (young birches)
,,	Pandemis ribeana Hb.	Larva on deciduous trees
,,	Paedisca corticana Hb.	Larva on oak
,,	Phalera bucephala L.	Larva on birch, etc., defoliating a young birch in VII. 23
,,	Salebria betulae Goeze.	Larva on birch (young birches)
,,	Scoparia ambigualis Tr.	Larva on moss. Adult hides on trunks*§
,,	S. frequentella Stt.	,, ,, ,,
,,	Swammerdamia heroldella Tr.	Larva on birch. Adult hides on trunks
,,	Talaeporia tubulosa Retz.	Larva on lichens on trunks*§
,,	Tinea parasitella Hb.	Larva in birds' nests
,,	T. semifulvella Hw.	,, ,,
,,	Tischeria complanella Hb.	Larva on oak
,,	Tortrix loeflingiana L.	Larva on deciduous trees (young birches)§
,,	T. viridana L.	Larva on oak
,,	Xenolechia humeralis Z.	?
	COLEOPTERA	
Beetle	Athons haemorrhoidalis F.	Larva on roots§
,,	Attelabus curculionides L.	Larva on young oak
,,	Byturus tomentosus F.	Larva in flowers of *Rubus*
,,	Coccinella 7-punctata L.	Larva feeds on aphides§
,,	C. 10-punctata L.	,, ,, §
,,	Cryptocephalus parvulus Müll.	Larva on birch
,,	Ernobius mollis L. (agg.)	?
,,	Halyzia 18-guttata L.	Larva on aphides§
,,	Hoplia philanthus Füss.	Larva on roots of plants
,,	Luperus rufipes Scop.	Birch
,,	Phyllobius argentatus L.	Deciduous trees
,,	P. pyri L.	,, ,, §
,,	Phyllodecta vitellinae L.	Larvae on aspen
,,	Rhagonycha fulva Scop.	Predaceous
,,	Serica brunnea L.	Larva on roots
,,	Strangalia armata Hbst.	Larva on decaying wood
	HEMIPTERA	
Bug	Aetorhinus angulatus Fall.	Young birches
,,	Anthocoris nemorum L.	Aphides
,,	Deraeocoris ruber L.	*Rubus* and various herbs
,,	Orthotylus flavinervis Kb.	Alder
,,	Plagiognathus chrysanthemi Wolff.	Various herbs
,,	P. arbustorum F.	Various herbs (e.g. *Teucrium*)
Leafhopper	Aphrophora alni Fall.	Deciduous trees
,,	Batracomorphus lanio L.	Oak
Psyllid	Psylla försteri Flor.	Alder
	NEUROPTERA	
Lacewing	Chrysopa perla L.	Larva on aphids (young birches)
,,	Ch. vulgaris Schneider	,, ,, ,,

Table VII (*continued*)

	ACARINA	
Mite	Eriophyes nalepai Focken	Gall on alder
	ARACHNIDA	
Spider	Epeira diadema L.	Web on young birches
	AVES	
Cuckoo	Cuculus canorus canorus L.	Insects
Robin	Erithacus rubecula melophilus Hart.	,,
Jay	Garrulus glandarius rufitergum Hart.	Mainly a general carnivore*§
Green Woodpecker	Picus viridis virescens Brehm.	Ants, etc.*§
Stonechat	Saxicola torquatus hibernaus Hart.	Mainly insects
	MAMMALIA	
Mouse	Apodemus silvaticus L.	(Probably) mainly herbivorous

Table VIII. *Inhabitants of* Polyporus betulinus

	HYMENOPTERA	
	A Proctotrupid beetle parasite	
	COLEOPTERA	
Beetle	Atheta aequata Er.	? Carnivorous
,,	A. cauta (parva) Er.	,,
,,	A. fungivora Th.	,,
,,	A. sericea Muls.	,,
,,	Cis bilammellatus Wood.	Fungus
,,	Coninomus nodifer Westw.	,,
,,	Litargus connexus Geoff. (bifasciatus)	,,
,,	Octotemnus glabriculus Gyll.	,,
,,	Proteinus ovalis Steph.	? Carnivorous
	COLLEMBOLA	
Springtail	Collembola common	Vegetarian and scavenger

Table IX.

Animals under bark of dead birches (B.), and chestnuts (C.)

	DIPTERA		
Fly	Larva of Forcipomyia pallida Winn.	C. (B. ? same species).	Scavenger
	COLEOPTERA		
Beetle	Atheta aequata Er.	B.	Scavenger
,,	Cerylon histeroides F.	B.	Larva carnivorous
,,	Cis vestitus Mel.	B.	Fungus eater
,,	C. villosulus Marsh.	B.	,,
,,	Ditoma crenata F.	B.	Larva carnivorous
,,	Dromius quadrinotatus Pz.	C.	Carnivorous
,,	Helops striatus Fourc.	C.	? Scavenger. Larva, cf. Table II
,,	Homalium rivulare Pk.	C.	? Carnivorous
,,	Litargus connexus Geoff. (bifasciatus)	C. B.	Fungus eater
,,	Melasis buprestoides L.	C.	Rotten wood of deciduous trees
,,	Ocypus morio Gr.	C.	Carnivorous
,,	Pteryx suturalis Heer.	B.	Fungus eater
,,	Phyllodrepa vilis Er.	C.	Fungus eater? or carnivorous
,,	Rhinosimus planirostris F.	C.	?
,,	Rhizophagus bipustulatus F.	C. B.	Carnivorous on bark beetles
,,	Scolytus intricatus Ratz.	C.	Wood of deciduous trees
,,	Silpha atrata L.	C.	? Carnivorous
,,	Silvanus unidentatus Ol.	B.	Larva ? carnivorous
,,	Thectura cuspidata Er.	B.	Feeds on Collembola

Table IX (*continued*).

	HEMIPTERA		
Bug	Aneuris laevis F.	C.	?
,,	Piezostethus cursitans Fall.	B.	? Carnivorous
,,	Xylocoris ater Duf.	C.	,,
	COLLEMBOLA		
Springtails	Collembola (unnamed) abundant	C. B.	Wood and fungus
	THYSANOPTERA		
	Thrips (unnamed bark species)	C.	?
	NEUROPTERA		
Snake fly	Rhaphidia sp.	C. B.	Larva carnivorous under bark
	ARACHNIDA		
Spider	Epeira umbratica Clk.	C.	Lives under bark, but catches insects from outside
,,	Salticus scenicus Clk.	C.	Hibernates under bark, in summer hunts on trunks
,,	Zilla atrica C.L.K.	C.	Carnivorous
	CRUSTACEA		
Woodlouse	Philoscia muscorum Swp.	C.	Scavenger and ? carnivorous
,,	Porcellio scaber Latr.	C. B.	,, ,,
	MOLLUSCA		
Slug	Arion subfuscus Drap.	C. B.	Scavenger
,,	Limax maximus L.	B.	,,
Snails	Polita alliaria Müll.	B.	,, ?

Table X. *Animals found in* Molinia *with dead birch leaves. Inner circle* 26. XII. 25.

	DIPTERA	
Fly	Limosina moesta Villen.	? Scavenger; abundant
	COLEOPTERA	
Beetle	Notiophilus biguttatus F.	Carnivorous
,,	Olophrum piceum Gyll.	,, ?
,,	Othius myrmecophilus Kies.	,, ?
	CHILOGNATHA	
Centipede	Scolopendra sp.	Carnivorous. Common
	CRUSTACEA	
Woodlouse	Philoscia muscorum Scop.	Scavenger and carnivorous. Common
	MOLLUSCA	
Slugs	Eggs probably of slugs	Common
	MAMMALIA	
Mouse	Apodemus silvaticus L. (probably)	Runs very numerous. Mainly vegetarian

Table XI. *Insect visitors of* Teucrium scorodonia.

M. = Male. F. = Female. W. = Worker

	HYMENOPTERA		
Humble Bee	Bombus agrorum F.	W.	Common
,,	B. hortorum L.	M.	,,
,,	B. lapidarius L.	M.	
,,	B. lucorum L.	M.	
,,	B. ruderarius Müll. (derhamellus K.)	W.	
Bee	Saropoda bimaculata Pz.	M. F.	Common
	DIPTERA		
Fly	Hylos culiciformis F.	Cf. Table VII	

E. THE GREAT HOLLOW.

In its animals, just as in its plants, this area has a special character. The greater number of the animal communities on the Common are represented in it. It is of interest to note that just as colonisation by oak, birch, and *Castanea* has proceeded further here than elsewhere, so the animals of deciduous woods are better represented. Some, such as *Scoparia* spp., are mainly typical of older woods, and others such as *Endotricha flammealis* Schiff., do not arrive, as a rule, till fairly late in succession. The peculiar character of the hollow, however, is probably most clearly seen in the greater abundance of insect life in general. This it probably owes mainly to its sheltered position, but partly to the fact that it acts as a trap to many of the smaller forms. The damp spots at the bottom of the hollow, besides allowing *Juncus* to grow, support several animals which are characteristic of the wetter areas (see Table XII).

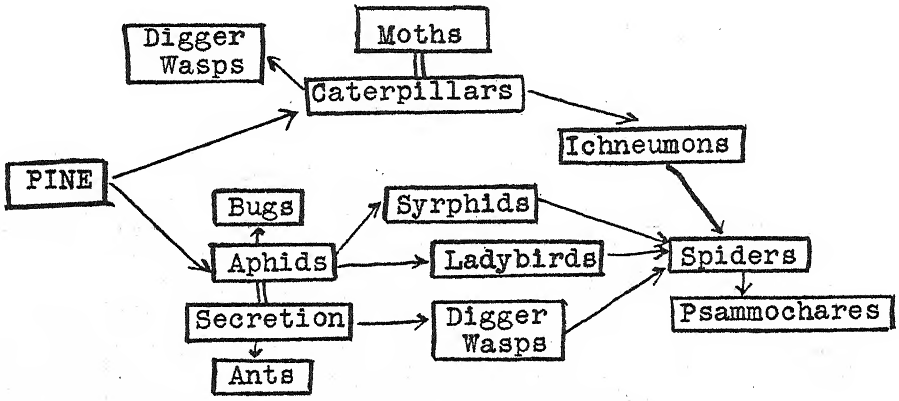

FIG. 1. Food-cycle on young pine.

At the other end of succession there has been a considerable growth of *Pinus* and a number of pine insects have been recorded. The regular pine ant, however, *Formica rufa* L. has not yet arrived. The most important herbivore on the pines is the aphid *Dilachnus pini* L. This is fed on by bugs (*Anthocoris nemorum* L.), ladybirds, and syrphid larvae. Spiders build their webs all over the pines and catch the winged individuals of the aphides, and also the adults of their enemies. The various digger wasps which visit the aphides for their secretions also get caught by the spiders. Finally digger wasps prey on the spiders. Such a community can be found on most of the young pines, even isolated ones in the damp areas, but is best developed in the Great Hollow. A rough diagram of the food relations is given in Fig. 1: the species concerned will be found in Table XIII.

Probably parasites rather than carnivores are the main check on many of the animals. But since the parasites are probably often controlled by carnivores the diagram represents a broad approximation to the truth. Thus, when

a spider is said to eat a moth, it may often eat mainly the parasites of the moth. As far as the total food supply is concerned the result is the same. The moth *Retinia* which feeds on the pine is particularly important because the larvae destroys the growing tip; if the moth were sufficiently abundant it might retard growth enough to modify or at least slow down succession.

When *Pinus* invades a birch scrub successfully a few of the birches generally survive in the pinewood. These continue to support a number of the birch insects; in Table VII such insects, still remaining in the pinewood at Oxshott, are marked with a symbol.

Table XII. *Animals typical of wetter areas which occur in the Great Hollow.*

	LEPIDOPTERA	
Moth	Coleophora caespititiella Z.	Larva on *Juncus effusus*
	COLEOPTERA	
Beetle	Crepidodera ferruginea Scop.	Vegetarian
,,	Cytilus varius F.	?
	HEMIPTERA	
Bug	Nabis rugosus L.	Carnivorous
Leafhopper	Philaenus lineatus L.	Vegetarian
	AMPHIBIA	
Toad	Bufo vulgaris aur. L. (?)	Young (perhaps really the Natterjack *B. calamita* Laur.)

Table XIII. *Animals on young pines in the Great Hollow.*

	HYMENOPTERA	
Ant	Acanthomyops niger L.	Secretions of aphides
Digger wasp	Crossocerus wesmaeli V. de Lind.	Secretions of aphides. Cf. Table I
Ant	Formica fusca L.	,, ,, ,,
Digger wasp	Oxybelus uniglumis L.	,, ,, ,,
,,	Psammochares fuscus L. (viaticus) and spp.	Catches spiders for its larvae
,,	Psen spp.	Secretions of aphides
,,	Sphex sabulosa L.	Caterpillars, e.g. larva of *Panolis*
Bees	Various bees coming to secretions of aphides caught by spiders	
Parasitic wasps	Numerous ichneumons (unnamed) are similarly caught	
	DIPTERA	
Fly	Syrphus vitripennis Mg. and spp.	Larva on aphides
	LEPIDOPTERA	
Moth	Gelechia dodecella L.	Larva on *Pinus*
,,	Ocnerostoma piniariella Z.	,,
,,	Panolis griseovariegata Goeze	,,
,,	Retinia buoliana Schiff.	,,
	COLEOPTERA	
Ladybird	Adalia bipunctata L.	Aphides
,,	Anatis ocellata L.	,,
,,	Coccinella 7-punctata L.	,,
,,	Exochamus quadripustulatus L.	,,
Beetle	Myelophilus piniperda L.	Burrows in shoots of *Pinus*
Bug	Anthocoris nemorum L.	Aphides
Aphid	Dilachnus pini L.	*Pinus.* (Probably there are other species of aphides)
	ARACHNIDA	
Spider	Agelena labyrinthica Cl.	Insects. Very common in summer
,,	Linyphia triangularis Cl.	Insects. Autumn

2. DAMP SERIES

A. Aquatic communities.

The Black Pond is the only large permanent body of water on the Common and has a rich aquatic life, forming a relatively self-contained community, which, however, has scarcely been studied. The dragonflies which breed there range all over the Common, becoming more abundant as the pond is approached, so that there must be a gradient in whatever biotic effects these highly carnivorous insects produce. Most of the dragonflies recorded have been seen by me and are common; others are recorded by Lucas (1900) as common at the right time of the year. A number of other species, only occurring as strays, have not been included. The incompleteness of the records for the Black Pond is obvious in the list, where practically no food for the various carnivores is recorded. The reed swamp on the edge of the pond, also, has not been much investigated; the data for the pond and its margin are given in Tables XIV and XV. The Black Pond is of further importance in being at least the main source of insects for all the temporary pools.

These pools fall into a number of classes depending on their degree of permanence (which is usually correlated with their depth) and their distance from the Black Pond.

The shallower pools were first developed on the bare burnt soil of the Molinietum. When they dried up a dense carpet of *Funaria*, and later *Polytrichum*, was formed. If shallow pools are formed on this carpet they are unfavourable to animal life, and in any case the moss is so absorbent that there is little free water. Such pools, therefore, are a feature of early stages in succession (see Table XVI).

Deeper pools (9 in. to $2\frac{1}{2}$ ft.) are much more permanent, but they may dry up completely two or three times in the course of the summer. When they dry up they are carpeted by *Juncus supinus*, not by mosses. Such pools occur throughout the Molinietum and they have quite a rich fauna, especially when situated near the Black Pond. A number of insects are able to breed in the deeper pools and not in the shallower pools. The number of kinds and individuals of insects present depends directly on the length of time since the pool was last dried up. At the end of the wet summer of 1924 they had a particularly rich fauna (see Tables XVII and XVIII).

The work of Harnisch (1925) in Germany, Wesenberg-Lund (1921) in Denmark and Johannsen (1921) in Arctic Canada, shows that the community inhabiting such pools is very similar throughout the northern palaearctic region. Wesenberg-Lund has given an interesting account of the enemies of the mosquito larvae and pupae which are one of the main links in the food chain. A very tentative and incomplete food-cycle for the pools is given in the diagram (Fig. 2). The food relations are complicated because, in the case

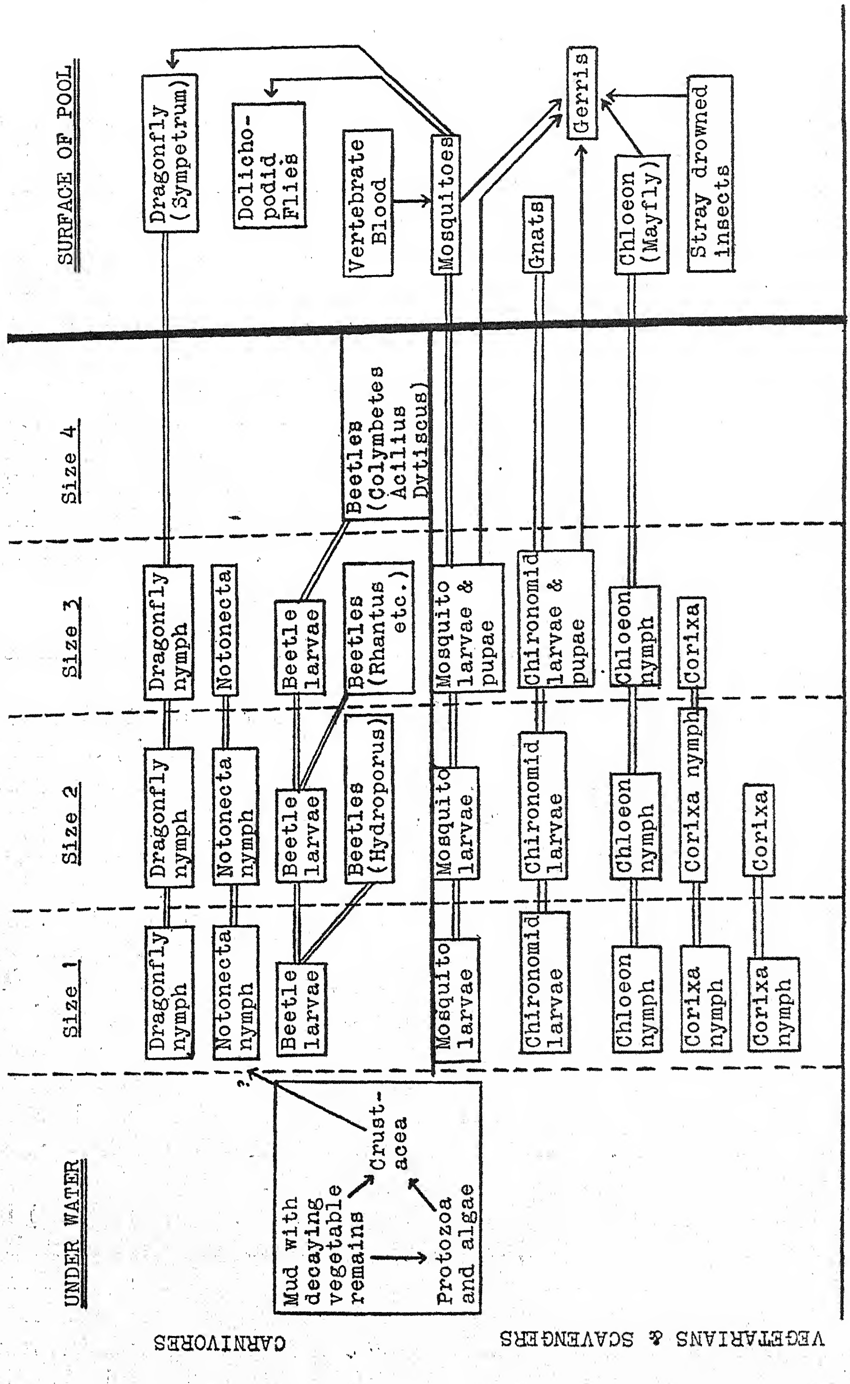
UNDER WATER
Size 1
Size 2
Size 3
Size 4
SURFACE OF POOL
CARNIVORES
VEGETARIANS & SCAVENGERS
Mud with decaying vegetable remains
Protozoa and algae
Crust-acea
?
Dragonfly nymph
Notonecta nymph
Beetle larvae
Mosquito larvae
Chironomid larvae
Chloeon nymph
Corixa nymph
Notonecta
Beetles (Hydroporus)
Corixa
Beetles (Rhantus etc.)
Mosquito larvae & pupae
Chironomid larvae & pupae
Beetles (Colymbetes Acilius Dytiscus)
Dragonfly (Sympetrum)
Dolicho-podid Flies
Vertebrate Blood
Mosquitoes
Gnats
Chloeon (Mayfly)
Stray drowned insects
Gerris

Fig. 2.

of most water beetles and other aquatic insect larvae, it is almost certain that the main factor deciding the food of the carnivore is its size. Many larvae are cannibals and will eat smaller larvae of their own species. A scheme has been adopted which attempts to show the relation of size to the food chain. Among the beetles there are three main sizes, though these are not, of course, sharply marked off, represented by *Hydroporus*, *Agabus* and *Colymbetes-Dytiscus* respectively. The largest type of larva, of course, grows through all the other sizes. In the diagram the thick vertical line represents the surface of the water. The horizontal line divides the aquatic community into carnivores and refuse-eaters. The vertical dotted lines divide the animals into four size-groups, representing either different sizes of the adults, or sizes passed through by growing larvae. The carnivores in any one size-group will eat all the carnivores smaller than themselves, and any refuse-eater up to their own size. Thus a carnivore will eat any other carnivore to the left of it in the diagram and any refuse feeder to the left of it or vertically beneath. Further investigation would probably show that specialisation exists amongst the carnivores in their choice of food and also perhaps that the largest forms would neglect the smallest food animals and only pay attention to those nearer to them in size.

Table XIV. *Animals noticed in the Black Pond.*

		HEMIPTERA
Bugs	Arctocorisa fabricii Fieb.	Scavenger and ? partly carnivorous
,,	A. hieroglyphica Duf.	,, ,, ,,
,,	A. moesta Fieb.	,, ,, ,,
,,	Callicorixa praeusta Fieb.	,, ,, ,,
,,	Corixa geoffroyi Leach	,, ,, ,,
		TRICHOPTERA
Caddis	Phryganea varia F.	Larva carnivorous
,,	Polycentropodidae ? sp.	,, ?
		ODONATA
Dragonfly	Aeschna cyanea Müll.	Larva carnivorous. Adult carnivorous above pond, etc.
,,	A. grandis L.	,, ,, ,, ,,
,,	A. juncea L.	,, ,, ,, ,,
,,	A. mixta L.	,, ,, ,, ,,
,,	Agrion puella L.	,, ,, ,, ,,
,,	Anax imperator Leach	,, ,, ,, ,,
,,	Cordulia aenea L.	,, ,, ,, ,,
,,	Enallagma cyathigerum Charp.	,, ,, ,, ,,
,,	Leucorhinia dubia Lind.	,, ,, ,, ,,
,,	Libellula depressa L.	,, ,, ,, ,,
,,	L. quadrimaculata L.	,, ,, ,, ,,
,,	Pyrrhosoma nymphyla Sulz.	,, ,, ,, ,,
,,	P. tenella Vill.	,, ,, ,, ,,
,,	Sympetrum scoticum Don.	,, ,, ,, ,,
		AVES
Moorhen	Gallinula chloropus chloropus L.	Mainly aquatic plants
Coot	Fulica atra atra L.	,,

Table XV. *Animals in the reed swamp at the edge of the Black Pond.*

		DIPTERA
Fly	Leptis scolopacea L.	Larva subterranean, carnivorous. Adult carnivorous
		LEPIDOPTERA
Moth	Crambus pascuellus L.	Larva on grasses
,,	C. pratellus L.	,,
,,	C. tristellus F.	,,
		COLEOPTERA
Beetle	Acupalpus meridianus L.	Carnivorous
,,	Coccidula rufa Abst.	,,
,,	C. scutellata Hbst.	,,
,,	Cyphon padi L.	Larva aquatic ? carnivorous
,,	Plectroscelis concinna Marsh.	Cruciferae
		AVES
Snipe	Capella gallinago gallinago L.	Subaquatic insects, worms, etc.

Table XVI. *Shallow temporary pools.*

		COLEOPTERA
Beetle	Agabus bipustulatus L.	Carnivorous
,,	Helophorus affinis Marsh.	? Vegetarian. This species may even occur in foot-marks
,,	Hydroporus melanarius Stm.	Carnivorous
,,	H. planus F.	,,
,,	H. pubescens Gyll.	Carnivorous. This species may aestivate in the dried mud

Table XVII. *Deeper temporary pools with* Juncus supinus.

		DIPTERA	
Mosquito	Aedes annulipes Mg.	Larva vegetarian and scavenger	
Gnats	Chironomids. None identified		
Fly	Caenia albula Mg.	? Adult on the surface	
,,	Campsicnemus scambus Fall.	Carnivorous, on the surface	
,,	Dolichopus vitripennis Mg.	,,	,,
,,	Hydrophorus bipunctatus Lehm.	,,	,,
,,	Octhera mantis DeG.	,,	,,
		COLEOPTERA	
Beetle	Acilus sulcatus L.	Carnivorous, on the surface	
,,	Agabus chalconotus Pz.	Carnivorous (especially where there is much dead grass)	
,,	A. bipustulatus L.	Carnivorous. Very common	
,,	Anacaena limbata F.	? Vegetarian	
,,	Berosus luridus L.	,,	
,,	Colymbetes fuscus L.	Carnivorous. Common	
,,	Dytiscus marginalis L.	,,	
,,	Gyrinus natator Scop.	Carnivorous, on the surface	
,,	Helochares punctatus Shp.	? Vegetarian	
,,	Helophorus affinis Marsh	,,	
,,	Hydroporus discretus Fair.	? Carnivorous	
,,	H. erythrocephalus L.	,,	
,,	H. gyllenhali Schiödte	,,	Common
,,	H. neglectus Schaum.	,,	
,,	H. planus F.	,,	
,,	H. pubescens Gyll.	,,	Common
,,	Ibybius aenescens Th.	Carnivorous	
,,	Rhantus bistriatus Berg.	,,	
,,	R. pulverosus Steph.	,,	

Table XVII (*continued*)

	HEMIPTERA		
Bug	Arctocorisa fabricii Fieb.	? Scavenger and partly carnivorous.	Common
,,	A. fallenii Fieb.	,, ,, ,,	
,,	A. hieroglyphica Duf.	,, ,, ,,	Common
,,	A. limitata Fieb.	,, ,, ,,	
,,	A. moesta Fieb.	,, ,, ,,	Common
,,	A. sahlbergi Fieb.	,, ,, ,,	
,,	A. semistriata Fieb.	,, ,, ,,	
,,	A. striata L.	,, ,, ,,	
,,	Callicorixa praeusta Fieb.	,, ,, ,,	
,,	Corixa geoffroyi Leach	,, ,, ,,	Common
,,	Hygrotrechus (Gerris) paludum F.	Carnivorous, on the surface	
,,	Limnotrechus (G.) gibbifer Schum.	,, ,,	
,,	L. lacustris L.	,, ,,	Common
,,	L. odontogaster Zett.	,, ,,	
,,	Notonecta furcata F.	Carnivorous	
,,	N. glauca L.	,,	Common
,,	N. halophila Edw. (viridis Delc.)	,,	
,,	N. maculata F.	,,	Common
	EPHEMEROPTERA		
Mayfly	Chloeon dipterum L.	Larva vegetarian	
	ODONATA		
Dragonfly	Sympetrum sp.	Larva carnivorous	
	ARACHNIDA		
Spider	Tetragnatha sp.	Carnivorous, on rushes at edge	
	AMPHIBIA		
Frog	Rana temporaria L.	Carnivorous (not breeding here?)	

Table XVIII. *In* Juncus supinus *of dried pools.*

	LEPIDOPTERA		
Moth	Coleophora glaucicolella Wood	Larva on *Juncus*	
,,	Gliphipteryx thrasonella Scop.	,,	Abundant
	COLEOPTERA		
Beetle	Aculpalpis dorsalis F.	Carnivorous	
,,	Bembidium lampros Hbst.	,,	
,,	Pterostichus diligens Stm.	,,	
,,	P. nigrita F.	,,	
	HEMIPTERA		
Bug	Acanthia saltatoria L.	Carnivorous	
,,	Limnotrechus gibbifer Schum.	(Aestivating)	
	CRUSTACEA		
Woodlouse	Porcellio scaber Latr.	Scavenger and carnivorous	
	ARACHNIDA		
Spider	Erigone atra Bl.	Carnivorous	

Another set of animals lives in the drains that were dug across the Common after felling. In the drains which are choked with dead leaves of *Molinia* the only insect that has been noted is the beetle *Agabus chalconotus* St. Many of the drains however are more like small streams and have a proper aquatic vegetation, consisting of *Glyceria fluitans*, *Polygonum polygonifolius* and much *Spirogyra*. Similar ditches on other London heaths have been found to have a nearly identical fauna (Table XIX). The edge of these drains has also a very characteristic set of animals, some of which are found nowhere else on the Common (Table XX). A number of flies with aquatic or semi-aquatic

larvae probably breed in these ditches. The adults are either flower-haunting bee-flies (*Eristalis*) or blood-suckers (Tabanids) and are found all over the Common. The species that have been recorded are given in Table XXI.

Table XIX. *Insects in the ditches.*

		DIPTERA		
Fly	Gymnopternus nanus Mcq.	Carnivorous	22	Stream with dense growth of *Glyceria* in the mixed wood. The numbers give proportions of a random sample from the surface
,,	Hydrellia griseola Fall.	Larva on grasses	11	
,,	Limosina humida Hal.	?	24	
,,	Parhydra aquila Fall.	?	2	
,,	P. coarctata Fall.	?	2	
,,	P. quadripunctata Mg.	?	8	
		COLEOPTERA		
Beetle	Agabus bipustulatus L.	Carnivorous		
,,	A sturmii Gyll.	,, Common		
,,	Anacaena globulus Pk.	? Vegetarian		
,,	A. limbata F.	,,		
,,	Helophorus affinis Marsh.	,,		
,,	Hydrobius fuscipes L.	,,		
		HEMIPTERA		
Bug	Arctocorisa fabricii Fieb.	Scavenger and ? partly carnivorous		
,,	A. sahlbergi Fieb.	,, ,, ,,		
,,	Velia currens F.	Carnivorous, on the surface		
		ODONATA		
Dragonfly	Aeschna juncea L. la.	Carnivorous		
,,	Agrionid la.	,,		
		TRICHOPTERA		
Caddis	Polycentropodidae la.	Carnivorous		

Table XX. *In vegetation at the edges of ditches.*

	COLEOPTERA		
Beetle	Agononum oblongum F.	Carnivorous	
,,	Bembidium lampros Hbst.	,,	
,,	Lathrobium brunnipes F.	,,	
,,	L. terminatum Gr.	,,	Common
,,	Olophrum piceum Gyll.	,,	
,,	Pterostichus minor Gyll.	,,	Common
,,	P. strenuus Pz.	,,	
,,	Stenus ossium Steph.	,,	
,,	S. rogeri Kr.	,,	
	COLLEMBOLA		
Springtails	Collembola common	Vegetarian and scavengers	
	CRUSTACEA		
Woodlouse	Porcellio scaber Latr.	Scavenger and partly carnivorous	
	ARACHNIDA		
Spider	Centromerus prudens Cambr.	Carnivorous	
,,	Walckeraera nudipalpis Westr.	,,	

Table XXI. *Diptera with aquatic or subaquatic larvae.*

Fly	Chrysops coecutiens L.	Larva carnivorous.	Bloodsucker	
,,	Eristalis arbustorum L.	Larva scavenger.	On flowers	
,,	E. intricarius L.	,,	,,	
,,	E. pertinax Scop.	,,	,,	
,,	E. tenax L.	,,	,,	
,,	Haematopota pluvialis L.	Larva carnivorous.	Adult a bloodsucker	
,,	Helophilus hybridus Lw.	Larva scavenger.	Adult on flowers	
,,	Sericomyia borealis Fall.	,,	,, ,,	
,,	Tabanus bromius L.	Larva carnivorous.	Adult a bloodsucker	
,,	T. sudeticus Z.	,,	,,	,,
,,	Therioplectes distinguendus Verr.	,,	,,	,,
,,	T. tropicus Mg. var. bisignatus Jaenn.	,,	,,	,,

B. SPHAGNETUM.

Although this has not been much investigated, it is certainly poorly represented at Oxshott. Nearly all the *Sphagnum* was shaded by heavy woods before felling and so was unsuitable, and since the felling animals have been slow in arriving. The only insects that have been noted are the beetle *Cyclonotum orbiculare* F. and the bug *Microvelia reticulata* Burm. No doubt there is a large microfauna.

C. SUCCESSION ON BARE, WET AREAS.

In the earlier stages of succession there is no distinction in habitat between bare, wet areas and the margins of pools. Gradually, however, mosses form a carpet, which, when dense, becomes the habitat of a different set of animals. The animals characteristic of the early stages of succession still hang on at pool margins, in dried up pools and at damp spots on the paths. In the late summer of 1922 bare, wet areas were very extensive and the animals were those of a pond margin (e.g. *Loricera*, *Bembidium* spp.). In the winter of 1922–3 the ground was much flooded and the *Anchomenus*, *Loricera*, *Notiophilus biguttatus* F. and *Acanthia* were found hibernating under pine bark above the water level. In the summer of 1923 the bare areas were much smaller owing to the spread of *Funaria hygrometrica*; many of the pioneers, however, will tolerate the moss when it is short. The growth of moss is not regular, and does not begin quickly on areas often flooded, so that some bare areas existed in 1925.

In any spot where succession was watched *Bembidium lampros* Hbst. and *Pterostichus diligens* Stm. came in with the mosses and soon became abundant. The latter beetle hibernates in *Polytrichum* and not under pine bark. In 1924 the animals characteristic of bare, damp areas were much scarcer and various new animals appeared. Probably the community eventually changes into one of the normal damp ground series, but this has not yet happened in the places that have been watched. *Polytrichum* at any rate can remain as a local dominant for some years. These facts are summarised in Table XXII. The four stages shown are (1) the bare ground stage, (2) young *Funaria*, (3) *Funaria*, *Ceratodon* and *Polytrichum*, (4) *Polytrichum*. *Ceratodon* may be the main moss where the ground is a little drier, and here the digger wasps *Priocnemis parvulus* Dahlb. (commonly), *Psammochares fuscus* L. (*viaticus*) and *Gorytes quadrifasciatus* F. are found nesting.

The arrival of *Carabus*, the large apterous predaceous beetle, is probably partly correlated with the first abundance of molluscs and earthworms on which it commonly feeds. All these forms are mainly found under bark of pine, etc., in the damp areas, but come out at night. In the following table the correlation between the arrivals is shown:

		1923	1924	1925
Molluscs	Limax maximus L.	A few	A few	Common
	Arion ater L.	,,	Common	,,
	A. subfuscus Drap.	,,	,,	,,
	Polita alliaria Müll.	—	—	A few
Earthworms		—	A few	Common
Beetle	Carabus catenulatus Scpp.	—	One	,,

Table XXII. *Succession on bare, wet areas.*

1 = Summer 1922. 2 = Summer 1923. 3 = Summer 1924. 4 = Summer 1925

			1	2	3	4
	COLEOPTERA					
Beetle	Amara lunicollis Schiödte	Carnivorous	—	2	—	—
,,	Anchromenus 6-punctatus L.	,,	1	2	3	—
,,	Bembidium biguttatus F.	,,	—	2	—	—
,,	B. bruxellense Wesm.	,,	1	—	—	—
,,	B. lampros Hbst.	,,	1	2	3	4
,,	B. riparium Ol.	,,	1	—	—	—
,,	Carabus catenulatus Scop.	,,	—	—	—	4
,,	Cytilus varius F.	?	1	2	—	4
,,	Haltica oleracea L.	Larva on *Epilobium*	—	—	3	4
,,	Loricera pilicornis F.	Carnivorous	1	—	—	—
,,	Megasternum boletophagum Marsh	Scavenger	—	—	—	4
,,	Notiophilus biguttatus F.	Carnivorous	1	2	3	4
,,	N. palustris Duft.	,,	1	—	—	—
,,	Pterostichus angustatus Duft.	,,	—	—	3	—
,,	P. diligens Stm.	,,	—	2	3	—
,,	P. nigrita F.	,,	—	2	—	—
,,	Stenus longitarsis Th.	,,	1	—	—	—
,,	S. rogeri Kr.	,,	1	—	—	—
,,	Tachyporus chrysomelinus L.	,, ?	1	?	3	—
,,	T. hypnorum F.	,, ?	1	?	3	—
	HEMIPTERA					
Bug	Acanthia saltatoria L.	Carnivorus ?	1	2	—	—
,,	Nabis rugosus L.	,,	—	—	3	—
,,	Trapezonotus arenarius L.	?	1	?	—	—
	COLLEMBOLA					
Springtails	Collembola abundant	Vegetarian	?	?	?	4
	ORTHOPTERA					
Grasshopper	Tettix bipunctatus L.	Vegetarian	1	2	—	—
	CRUSTACEA					
Woodlouse	Porcellio scaber Latr.	Scavenger and ? carnivorous	—	—	—	4
	ARACHNIDA					
Spider	Erigone atra Bl.	Carnivorous	—	2	—	—
,,	Lycosa amentata Cl.	,,	1	—	—	—
,,	Oedothorax fuscus Bl.	,,	—	2	—	—
,,	Pirata piraticus Cl.	,,	1	—	—	—
,,	Tarentula barpipes Sund.	,,	1	—	—	—
,,	Trochosa ruricola DeG.	,,	1	—	—	—
,,	Young of Lycosa, Tibellus, Pirata	,,	1	—	—	—
,,	Young of Xysticus sp.	,,	1	?	?	4
	ANNELIDA					
Earthworms		Vegetarian	—	—	—	4
	MOLLUSCA					
Slug	Limax maximus L.	Scavenger	—	—	—	4
Snail	Polita alliaria Müll.	? Carnivorous	—	—	—	4

D. MOLINIETUM.

Before the fire in 1921 there was an extensive growth of *Molinia* and, since much of it was not destroyed, the animal community connected with it was fully developed when the Common was first visited in 1922; there are thus no observations on the actual changes resulting from the growth of *Molinia* on a given area. The fauna is not unlike that of an ordinary meadow, though there are a number of peculiar forms. Some of the bugs, e.g.

Stenodema and *Trigonotylus* and leafhoppers, e.g. *Tettigonia*, show typical adaptations to grass conditions in their colouring, and, in the case of the bugs, in their elongate shape. Grasshoppers are excessively abundant, and have increased in numbers since 1922. The grass-moths (*Crambus*) were exceedingly abundant in 1922 and to a less extent in 1923. Since then they have been relatively scarce. The same is true of the common rush feeding moth, *Bactra lanceolana* Hb. Perhaps they increased originally as a result of the hot summer in 1921; at any rate no other cause can be suggested. The animals recorded are given in Table XXIII.

The effect of invasion by *Betula* has been discussed in a previous section (p. 257). *Molinia* can grow for a long time in areas which have been invaded by pine. Such *Molinia*, growing in pinewoods, still has associated with it most of the small insects, etc., which normally live under the tufts, e.g. beetles, bugs, spiders and woodlice. The moths and grasshoppers disappear. Many of the fungus beetles of the pinewood hide in the tufts in winter; several weevils, probably attracted from neighbouring leguminous crops, hibernate in *Molinia* growing under the shade of pine. Many of the insects found in the *Calluna* growing in the same situation also occur.

Table XXIII. *Animals of the Molinietum.*

	DIPTERA	
Fly	Borborus geniculatus Mcq.	Hibernates in tufts. ? Scavenger
,,	Loxocera albiseta Schrk.	? ?
,,	Sepedon sphegeus F.	Common in autumn
,,	Sepsis spp.	Hibernate in tufts. Larva a scavenger
	LEPIDOPTERA	
Butterfly	Adopaea sylvanus Esp.	Larva on grasses
,,	A. thaumas Hufn.	,,
,,	Coenomympha pamphilus L.	,,
Moth	Crambus hamellus Thnbg.	Larva on grasses. Not common but characteristic
,,	C. pascuellus L.	Larva on grasses. Abundant
,,	C. tristellus L.	,,
Butterfly	Epinephele ianira L.	,,
Moth	Euxanthis hamana L.	
Butterfly	Heodes phloeas L.	Larva on *Rumex* spp.
Moth	Nomophila noctuella Schiff.	Larva on herbs
Butterfly	Pararge megaera L.	Larva on grasses
Moth	Plusia gamma L.	Larva on herbs
,,	Plutella maculipennis Curt.	,,
	COLEOPTERA	
Beetle	Bradycellus verbasci Duft.	Carnivorous
,,	Haltica oleracea L.	Larva on *Epilobium*. Adult hibernates in tufts
,,	Hoplia philanthus Füss.	Larva on plant roots
,,	Pterostichus strenuus Pz.	Carnivorous. Adult in tufts in winter
,,	Sitones lineatus L.	Leguminosae. Adult in tufts in winter
,,	Stenus flavipes Steph.	Carnivorous. Adult in tufts in winter. A characteristic species
,,	S. rogeri Kr.	Carnivorous
,,	Tachyporus chrysomelinus L.	Carnivorous ? Adult in tufts in winter
,,	T. hypnorum F.	,, ,, ,,

Table XXIII (*continued*).

	HEMIPTERA	
Bug	Nabis major Costa.	Carnivorous
,,	N. rugosus L.	,,
,,	Stenodema calcaratum Fall.	On grasses
,,	S. holsatum F.	,,
,,	Trigonotylus ruficornis Geoff.	,,
Leafhopper	Philaenus lineatus L.	
,,	Tettigonia viridis Liv.	,,
	COLLEMBOLA	
Springtails	Collembola. None identified	Vegetarian and scavengers
	ORTHOPTERA	
Grasshopper	Chorthippus elegans Charp.	Herbs
,,	C. parallelus Zett.	Herbs. A short winged form not becoming common before 1924
,,	Gomphocerus maculatus Thnbg.	Herbs. Abundant. With green forms
,,	Metrioptera brachypterus L.	,, Abundant
,,	Omocestus viridulus L.	,,
,,	Stauroderus bicolor Charp.	,, Commonly with green forms
	ARACHNIDA	
Spider	Agelena labyrinthica Cl.	Mainly on bare areas, but catches grass insects, e.g. Philaenus
,,	Drassodes troglodytes C.L.K.	Carnivorous
,,	Linyphia clathrata Sund.	,,
,,	Lycosa amentata Cl.	,,
,,	Pisaura mirabilis Cl.	,,
,,	Segestria senoculata L.	,,
,,	Stemonyphantes lineatus L.	,,
,,	Tibellus oblongus Walck.	,,
,,	Xysticus erraticus Bl.	,,
	CRUSTACEA	
Woodlouse	Porcellio scaber Latr.	Scavenger and partly carnivorous
	AVES	
Skylark	Alauda arvensis arvensis L.	Mainly seeds
Kestrel	Falco tinnunculus tinnunculus L.	Mainly mice, partly young birds
Partridge	Perdix perdix perdix (L.)	Mainly plants. Partly insects in summer
Pheasant	Phasianus colchicus L.	,, ,, ,,
Stonechat	Saxicola torquata hibernans Hart.	Mainly insects
	MAMMALIA	
Hare	Lepus europaeus occidentalis de Winton	Vegetarian

E. JUNCETUM.

The *Juncus* fauna has not been fully worked out, but probably the number of species is rather low. In individuals, however, the actual rush-feeders are often exceedingly abundant. *Coleophora caespititiella* Zell. must destroy at least half the seeds produced. Some of these rush-feeders also occur on *J. squarrosus*, growing on drier areas, but the fauna given in Table XXV is that connected with *J. effusus*. A few insects are included which visit flowers growing commonly in the Juncetum.

Table XXIV. *Animal community in the Juncetum.*

	HYMENOPTERA	
Bee	Bombus lucorum L.	Female. On *Lotus uliginosus* and *Cirsium palustre*
,,	Megachile maritima K.	Male. Common on Lotus
,,	M. willughbiella K.	,, ,,
,,	Psen unicolor V. de Lind.	Female hunting leafhoppers amongst *Juncus*
,,	Psammochares? piliventris Mor. (cardui)	Female on Lotus
Wasp	Vespa germanica Fab.	Worker (probably fly-hunting) in *Juncus*
,,	V. vulgaris L.	,, ,, ,,
,,	V. rufa L.	,, ,, ,,

Table XXIV (*continued*).

	DIPTERA	
Fly	Dolichopus pennatus Mg.	Predaceous
,,	Gymnopternus nanus Mcq.	,,
,,	Tachydromia flavipes F.?	,,
,,	Psectrosciara coxendix Verr.	Adults, sometimes very common on heads of *Juncus*. Larva ? scavenger
	LEPIDOPTERA	
Butterfly	Adopaea silvanus Esp.	On flowers of *Lotus*
Moth	Bactra lanceolana Hb.	Larva on *Juncus*. Abundant 1922–3
,,	Coleophora caespititiella Zell.	,, ,, Abundant
,,	C. glaucicolella Wood	,, ,,
,,	Gliphipteryx thrasonella Scop.	,, ,, Common 1924–5
	COLEOPTERA	
Beetle	Crepidodera transversa Marsh	Vegetarian. Abundant in 1924
,,	Cyphon variabilis Thnbg.	Larva carnivorous
,,	Pterostichus stremus Pz.	Carnivorous
,,	Rhagonycha fulva Scop.	Carnivorous (sometimes on flowers of *Lotus*)
,,	Xantholinus linearis Ol.	? Carnivorous
	HEMIPTERA	
Bug	Anthocoris nemorum L.	Carnivorous
,,	Trigonotylus ruficornis Geoff.	Vegetarian
Leafhopper	Athysanus sordidus Zett.	,,
,,	Conomelus limbatus Fab.	,, Abundant
,,	Limotettix antennata Boh.	,,
	ARACHNIDA	
Spider	Chromolithus festivus C.L.K.	Carnivorous. Web on heads of *Juncus*
,,	Dictynna luteus F.	,, ,, ,,
,,	Pisaura mirabilis Cl.	Carnivorous

F. SPECIAL PLANTS.

Certain plants characteristic of wet areas always have certain animals, either vegetarians or flower visitors, associated with them. These animals certainly seek the plant rather than any special conditions and so are given separately rather than in the community in which the plant grows. Thus the flowers of *Potentilla erecta* are always visited abundantly by the fly *Hercostomus nigripennis* Fall; and the bees *Prosopis brevicornis* Nyl. and *P. genalis* Thoms., occasionally by workers of *Bombus agrorum* Fab.

Rumex acetosella is the food of the beetles *Cryptocephalus fulvus* Goeze, *Apion rubens* Steph. and *Rhinoncus castor* F. These are found with the plant wherever it occurs.

Ragwort (*Senecio jacobaea*) and other species of *Senecio* are fed on by the beetle *Longitarsus jacobeae* Wat., and the flowers of this and other Yellow Composites are visited by the fly *Sicus ferrugineus* L. and bees of the genus *Halictus*.

The species connected with *Salix* (broad-leaved species), with *Ulex europaeus* and with *Rubus* are so numerous that they are given in Tables XXV, XXVI, and XXVII. The flowers of the first two plants are important as being the main source of food for the spring bees, and of various other hibernated insects.

Table XXV. *Animals connected with* Salix spp.

M. = Male. F. = Female. W. = Worker

	HYMENOPTERA		
Wasp	Ancistrocerus callosus Thoms.	On flowers	F.
Bee	Andrena albicans Müll.	,,	M. F.
,,	A. bimaculata K.	,,	M.
,,	A. clarkella K.	,,	M. F.
,,	A. dorsata K.	,,	M. F.
,,	A. fulva Schrk.	,,	F.
,,	A. gwynana K.	,,	M.
,,	A. parvula K.	,,	F.
Hive bee	Apis mellifera L.	,,	W.
Humble bee	Bombus agrorum F.	,,	F.
,,	B. jonellus K.	,,	F.
,,	B. lapidarius L.	,,	F.
,,	B. lucorum L.	,,	F.
,,	B. pratorum L.	,,	F.
,,	B. terrestris L.	,,	F.
Bee	Halictus minutus Zett.	,,	F.
,,	H. punctatissimus Sch.	,,	F.
Digger wasp	Psammochares fuscus L. (viaticus)	,,	F.
	DIPTERA		
Fly	Chilosia vulpina Mg.	,,	M.
,,	Chortophila muscaria Mg.	,,	M. F.
,,	Eristalis intricarius L.	,,	M.
,,	Orthoneura geniculata Mg.	,,	M.
,,	Platychirus albimanus F.	,,	M. F.
,,	Rhabdophaga saliciperda Duf.	Galls on the stems with two Chalcid parasites	
,,	Scatophaga stercoraria L.	On the flowers	M.
,,	Syrphus lasiophthalmus Zett.	,,	M. F.
	LEPIDOPTERA		
Moth	Cerura furcula L.	Larva on leaves	
Butterfly	Vanessa io L.	On the flowers	
	COLEOPTERA		
Beetle	Adalia bipunctata L.	On the flowers	
,,	Crepidodera aurata Marsh	Feeds on the leaves	
,,	Melanophthalma gibbosa Hbst.	On the flowers	
,,	Meligethes ovatus Stm.	,,	
	HEMIPTERA		
Bug	Anthocoris nemoralis F.	On the flowers	
,,	A. nemorum L.	,,	
Psyllid	Psylla salicicola Först.	Feeds on the leaves	

Table XXVI. *Animals associated with* Ulex.

M. = Male. F. = Female. W. = Worker

	HYMENOPTERA		
Sawfly	Abia lonicerae L.	On the flowers	F.
Bee	Andrena bimaculata K.	,,	M.
,,	A. dorsata K.	,,	M.
,,	A. gwynana K.	,,	M.
Hive bee	Apis mellifera L.	,,	W. abundant
Humble bee	Bombus agrorum Fab.	,,	F. common
,,	B. ruderarius Müll. (derhamellus)	,,	F.
Bee	Halictus flavipes F.	,,	F.
,,	H. punctatissimus Sch.	,,	F.
	DIPTERA		
Fly	Eristalis pertinax Scop.	,,	M. F.
,,	Euaresta conjuncta Lw.	Adult hibernates in *Ulex*	
,,	Platychirus albimanus F.	On the flowers	M. F.
,,	P. scutatus Mg.	,,	M.

Table XXVI (*continued*).

	DIPTERA	
Fly	Scatophaga stercoraria L.	On the flowers M.
,,	Syrphus auricollis Ztt.	,,
,,	S. cinctellus Zett.	,,
,,	S. lasiophthalmus Ztt.	,,
,,	S. punctulatus Verr.	,,
,,	S. torvus O.S.	,,
,,	Tephritis vespertina Lw.	Adult hibernates in gorse
	LEPIDOPTERA	
Moth	Laspeyresia ulicetana Hw.	Larva on gorse
,,	Scythris grandipennis Hw.	,,
	COLEOPTERA	
Beetle	Adalia bipunctata L.	On the flowers
,,	Apion ulicis Först.	Larva on the seeds
,,	Micrambe vini Pz.	Larva on the flowers
,,	Sitones regensteinensis Hbst.	Larva on *Ulex*
,,	S. tibialis Hbst.	,,
	HEMIPTERA	
Bug	Asciodema obsoletum Fieb.	On *Ulex*
,,	Dictyonota strichnocera Fieb.	,,
	ARACHNIDA	
Spider	Epeira cornuta Cl.	Webs of the young abundant on *Ulex* in the spring

Table XXVII. *Insect visitors of flowers of* Rubus fruticosus (*agg.*).

M. = Male. F. = Female. W. = Worker

	HYMENOPTERA	
Bee	Apis mellifera L.	W. abundant
,,	Bombus agrorum Fab.	F. W. common
,,	B. hortorum L.	M. W.
,,	B. lucorum L.	M. F. W. common
,,	B. pratorum L.	M. common. W. only where a scrub has developed
,,	B. ruderarius Müll. (derhamellus)	M. F.
,,	B. terrestris L.	M. F. W.
Digger wasp	Cerceris labiata F.	M. Cf. Table I
,,	C. rybyensis L.	M. ,,
Bee	Chelostoma campanularum K.	M.
,,	Coelioxys elongata Lep.	M. F. Parasite of *Megachile*
Digger wasp	Gorytes quadrifasciatus F.	M.
Bee	Halictus flavipes F.	F. Cf. Table I
,,	H. nitidiusculus K.	F.
Ruby wasp	Hedychridium minutum Lep.	Cf. Table I
Bee	Megachile circumcincta Lep.	F.
,,	M. maritima K.	M. Cf. Table I
,,	M. versicolor Smith	M.
,,	M. willughbiella K.	F. Cf. Table XXIX
Digger wasp	Nysson interruptus F.	M. Cf. Table I
Wasp	Odynerus pictus Curt.	F.
Bee	Osmia leucomelaena K.	F.
Digger wasp	Oxybelus uniglumis L.	M. F. Cf. Table I
Bee	Prosopis brevicornis Nyl.	M. F.
,,	P. communis Nyl.	M. F.
,,	P. confusa Nyl.	M. F. common
,,	P. genalis Thoms.	M. F. Cf. Table XXIX
Digger wasp	Psen shuckardi Wesm.	M. Cf. Table I
Bee	Psithyrus barbutellus K.	M. parasite of *Bombus hortorum*
,,	Ps. distinctus Perez.	M. parasite of *B. lucorum*
,,	Ps. quadricolor Lep.	M. common parasite of *B. pratorum*
,,	Saropoda bimaculata Pz.	M. F. common. Cf. Table I
Digger wasp	Sphex campestris Latr.	,, ,,
,,	S. sabulosa L.	M. common. F. Cf. Table I
,,	Tachysphex unicolor Pz.	M. Cf. Table I

Table XXVII (*continued*).

	Diptera	
Fly	Chilosia scutellata Fall.	Larva ? fungi
,,	Empis aestiva Lw.	Carnivorous
,,	Eristalis arbustorum L.	Cf. Table XXII
,,	E. intricarius L.	,,
,,	Fabriciella ferox Pz.	Larva parasite of large caterpillars
,,	Sicus ferrugineus L.	
,,	Volucella pellucens L.	Commensal of wasps
,,	V. plumata L.	Commensal of *Bombus*
	Lepidoptera	
Butterfly	Adopaea sylvanus Esp.	Cf. Table VII
,,	Epinephele janira L.	
	Coleoptera	
Beetle	Byturus tomentosus F.	Cf. Table VII
,,	Rhagonycha fulva Scop.	
,,	Strangalia armata Hbst.	Cf. Table VII
	Hemiptera	
Bug	Anthocoris nemorum L.	
,,	Plagiognathus arbustorum F.	Cf. Table VII

G. Pine Stumps and Fungi.

The pine stumps and the fungi connected with them form a relatively clear-cut habitat, occurring in every part of the area. Fungi are by no means all equally attractive to insects, and, though this has not been worked out in detail, it is mainly the species connected with the stumps that have a large fauna. The community is probably nearly the same as that which is associated with fungi in the pinewood. The animals at the base of the food chain are larvae of small flies and Collembola. The staphylinid beetles feed on these but there are no details of their feeding habits.

The pine stumps are the home of another set of animals which gradually destroy the stumps. There is probably a good deal of difference between the early stages of colonisation of fresh pine stumps and of those which have been burnt. This has not been much studied at Oxshott, but in a general way the effect of burning is to cut out the early stages of the succession. A number of animals, often highly specialised to life under bark, only occur under fresh stumps, or those not badly burnt. The beetle *Melanophila acuminata* DeG. which is peculiar to burnt pine stumps and usually arrives while the fire is still smoking, has not been seen at Oxshott, though recorded from other heaths in southern England.

The normal course of succession probably begins with arrival of Scolytid beetles (e.g. *Hylastes*). With them come their special enemies, such as the beetles belonging to the genus *Rhizophagus*, which feed on the Scolytids. In the solid wood *Asemum* and *Criocephalus* make their burrows. The holes formed allow fungi to enter and their mycelia soon become abundant under the bark and in the wood. With them come abundant Collembola and their enemies the staphylinid beetles, small carabids; probably the flat, bark-haunting bugs also feed on them. Quite soon queen ants arrive and make their nests under the bark, and later the workers begin to excavate their

galleries in every direction. These activities soon loosen the bark and a kind of humus collects beneath it. As soon as ants have become abundant the woodpeckers attack the stumps and are perhaps one of the most important agencies in their destruction. When the bark has become really loose the specialised bark animals disappear and their place is taken by an assemblage of forms that need a dark, damp habitat. Such are woodlice, molluscs, earthworms and the carabid beetles which prey on them. Probably at Oxshott a stump may disappear in about eight years but the length of time would vary very considerably with local conditions. Under the shelter of a pine wood the stumps might persist almost indefinitely, while in damp, exposed situations the decay is rapid.

The stumps are often an important addition to the habitat in which they are situated because they may be used by whatever animals occur as hibernation quarters (beetles, wasps, flies), nesting sites (digger wasps, ants, spiders) or as shelter by day in dry areas (molluscs, beetles). The existence of stumps probably allows various animals to maintain themselves in such a habitat as a Callunetum, animals which would normally have to wait for more mesophytic conditions to be established.

Sclerodermae have a little fauna of their own. They grow mainly in the birch-scrub stages and often contain the beetles *Atheta xanthoptera* Steph., *Cryptophagus lycoperdi* Hbst. and *C. punctipennis* Bris. Perhaps the first named feeds on the larvae of the Cryptophagi.

Table XXVIII. *Animals associated with fungi.*

	DIPTERA	
Fly	Chilosia longula Ztt.	Larva in *Boletus bovinus*
,,	Forcipomyia spp.	Can be bred abundantly from fungi
,,	Leria cineraria Lw.	Larva on fungus (*Sparassis crespa*)
,,	Limosina antennata Duda	,, ? (*Sparassis crespa*)
,,	L. luteilabris Rdi.?	,, ,, ,,
,,	L. parapusio Dahl.	,, ,, ,,
,,	Mycetophilids common	Larva on fungus
	COLEOPTERA	
Beetle	Aleochara brunneipennis Kr.	Carnivorous (*Lactarius turpis*)
,,	Atheta xanthoptera Steph.	,, ,,
,,	Autalia impressa Ol.	(*L. turpis*)
,,	Boletobius pygmaeus F.	Carnivorous
,,	B. trinotatus Er.	,, (*L. turpis*)
,,	Gyrophaena gentilis Er.	,,
,,	Philonthus marginatus F.	,, (*L. turpis*)
,,	Ph. proximus Kr.	,, ,,
,,	Ph. varians Pk.	,, ,,
,,	Proteinus brachypterus F.	,,
,,	P. ovalis Steph.	,, (*L. turpis*)
,,	Quedius cinctus Pk.	,, ,,
,,	Tachinus laticollis Gr.	,,
	ANNELIDA	
Earthworm		Vegetarian (*Polyporus schweinitzi*)
	MOLLUSCA	
Slug	Arion ater L.	Vegetarian eating *Boletus bovinus*

Table XXIX. *Animals associated with pine stumps.*

	HYMENOPTERA	
Ant	Acanthomyops niger L.	Nesting
,,	Formica fusca L.	,,
,,	Leptothorax acervorum F.	,, (early stages)
Bee	Megachile willughbiella K.	Probably nests in the very rotten wood
Ant	Myrmica spp.	Nesting
Bee	Prosopis genalis Thoms.	Probably nests in the very rotten wood
Digger wasp	Psen unicolor V. de Lind.	,, ,, ,,
Wasp	Vespa germanica F.	Females hibernating
,,	V. vulgaris L.	,,
	DIPTERA	
Fly	Exechia spinigera Winn.?	Larva on fungi
,,	Mycetophilus ocellus Walk.	Larva on fungi (adults sometimes hide under bark)
,,	Phaonia spp. and other muscids	Hibernating
,,	Tachypeza nubila Mg.	Larva carnivorous in rotten wood. Adult on small flies
	LEPIDOPTERA	
Moth	Oecophora sulphurella F.	Larva on rotten wood. Pupa under bark
	COLEOPTERA	
Beetle	Adalia bipunctata L.	Hibernating
,,	Agathidium laevigatum Er.	Fungus
,,	Anisotoma humeralis Kug.	,,
,,	Asemum striatum L.	Larva in solid wood
,,	Atheta aequata Er.	Carnivorous
,,	A. linearis Gr.	,, early stages of stumps
,,	Baptolinus alternans Gr.	,,
,,	Bradycellus harpalinus Dj.	Sheltering
,,	Cerylon histeroides F.	Larva carnivorous
,,	Coccidula spp.	Hibernating
,,	Conosoma pubescens Gr.	Carnivorous (later stages)
,,	Criocephalus ferus Kr.	Larva in solid wood (early)
,,	Ditoma crenata F.	Larva under bark, carnivorous (early)
,,	Dromius angustus Brulle	Carnivorous (early)
,,	Elater balteatus L.	Larva on rotten wood
,,	Helops striatus Fourc.	Probably mainly sheltering
,,	Homalium rivulare Pk.	Carnivorous. Mainly in fungi
,,	Hylastes ater Pk.	Larva in wood and bark (early stages)
,,	H. cunicularius Pk.	,, ,, ,,
,,	H. palliatus Gyll.	,, ,, ,,
,,	Leistus spinibarbis F.	Carnivorous (later stages)
,,	Leptusa fumida Er.	,, (early stages)
,,	Melanotus rufipes Hbst.	Larva on wood (early stages)
,,	Mycetoporus lucidus Er.	Carnivorous (fungi)
,,	Nebria brevicollis F.	,, (later stages)
,,	Ocypus morio Gr.	,,
,,	Pentarthrum huttoni Woll.	Larva on wood
,,	Phloeonomus punctipenne Th.	Carnivorous (early stages)
,,	Phloeopora reptans Gr.	,, ,,
,,	Phyllodrepa vilis Heer.	,, ,,
,,	Pissodes notatus F.	Larva on wood
,,	Pterostichus angustatus Duft.	Carnivorous. Burnt stumps
,,	P. vulgaris L.	,,
,,	Quedius maurus Sahlb. (fageti)	,,
,,	Rhizophagus bipustulatus F.	,, (early stages)
,,	R. ferrugineus Pk.	,, ,,
,,	Scaphisoma agaricinum L.	Fungi
,,	Silpha atrata L.	Carnivorous? (later stages)
,,	Sphindus dubius Gyll.	Fungi (early stages)
,,	Thanasimus formicarius L.	Carnivorous, esp. on dead trees
,,	Xantholinus linearis Ol.	,,
	HEMIPTERA	
Bug	Piezostethus cursitans Fall.	,, (early stages)

Table XXIX (*continued*).

	NEUROPTERA	
Snakefly	Rhaphidia maculicollis Steph.	Larva carnivorous (early stages)
	COLLEMBOLA	
Springtails	Collembola abundant	Vegetarian
	Campodea sp.	,,
	ARACHNIDA	
Spider	Agelena labyrinthica Cl.	Hibernating and making webs on the stumps when there are no bushes
,,	Prosthesima petiverii Scop.	Hiding egg cocoons
,,	Trochosa ruricola DeG.	,, and hibernating
,,	Salticus scenicus Cl.	Hunts on the stumps (catches *Oecophora*)
	CRUSTACEA	
Woodlouse	Porcellio dilatatus Brandt	Scavenger and partly predaceous (later stages)
,,	P. scaber Latr.	Scavenger and partly predaceous (later stages)
	CHILOGNATHA	
Centipedes	Lithobius spp. and others	Carnivorous. Common in later stages
	MOLLUSCA	
Slug	Arion ater L.	Vegetarian. Common in later stages
,,	A. subfuscus Drap.	,, ,, ,,
,,	Limax maximus L.	,, ,, ,,
	ANNELIDA	
Earthworms		Vegetarian. Common in later stages
	AVES	
Great Spotted Woodpecker	Dryobates major anglicus Hart.	Feeds on ants and other insects
Green Woodpecker	Picus viridis virescens Brehm.	,, ,, ,,
	MAMMALIA	
Rabbit	Oryctolagus cuniculus L.	Use the stumps as special depositories for dung

CONCLUSION

The animals found on the felled and burnt areas at Oxshott Common in the years 1922–5 have been recorded and some of their effects on one another, and of their relations to plant succession, have been described. It would be premature to make any generalisations about heath-animals.

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YEW COMMUNITIES OF THE SOUTH DOWNS

By A. S. WATT.

(With Plates IV and V, Folding Table, and seven Figures in the Text.)

CONTENTS.

This paper records an enquiry into the origin, structure, development and fate of some yew communities of the South Downs (Hants and Sussex); their relation to scrub, ash-oakwoods and beechwoods is discussed and evidence brought forward to show that these yew-woods are migratory societies of scrub.

The yew (*Taxus baccata*) is widespread on the chalk hills of West Sussex and East Hampshire, growing isolated in scrub, in ash-oakwoods and beechwoods, and in larger or smaller groups with or without other trees. In many cases at least the apparently fortuitous distribution of scattered yews can be explained in accordance with the findings of this study: it is, however, with the yew in the larger groupings that the paper mainly deals.

TOPOGRAPHY

The yew communities examined lie in the neighbourhoods of Butser Hill and Ditcham Park and of Goodwood, the former, an area familiar to students of chalk vegetation through the work of Tansley[1] and Adamson[1]—the latter the scene of the author's work on the Sussex beechwoods[2]. The following yew-woods have been examined. Opposite the name of each the aspect and locality are given:

1. Bottom "A," valley facing S. Southern slope of Butser Hill.
2. Bottom "B," valley facing S.E. and S.S.E. Southern slope of Butser Hill.
3. Kingley Vale, valley facing S. 4 miles N.W. of Chichester (Goodwood area).
4. Hillhampton Bottom, valley facing S.S.E. Southern slope of Butser Hill.
5. Wascombe Bottom, valley facing S.E. Southern slope of Butser Hill.
6. Chilgrove Hill, slope facing N.E. 2½ miles N.W. of West Dean (Goodwood area).
7. Downley Brow, slope facing N.W. 1 mile N.E. of Ditcham House.
8. Holt Down, slope facing N.W. 1 mile S.W. of Butser Hill.
9. Deep Combe, valley facing S.S.W. 1¾ miles N.E. of East Dean (Goodwood area).
10. Stead Combe, valley facing E. 1 mile W. of Cocking (Goodwood area).

A brief consideration of the geographical position of these yew-woods in relation to the large forest area of West Sussex and East Hampshire will be of value in helping to assign to the yew-woods their proper place in the context of South Down vegetation. Quite detached from the main body of woodland and set in a background of grassland are, to the south, Kingley Vale, and to the west, Bottoms "A" and "B," Hillhampton and Wascombe Bottoms and Holt Down. Deep Combe, Chilgrove Hill and Downley Brow are just on the outskirts of progressive woodland and may be continuous with the main body. Stead Combe in the Cocking Gap lies near the north escarpment in a region with much chalk grassland clothing the gentler slopes of the Gap and with progressive woodland in the neighbourhood. On the whole, therefore, the yew-woods studied grow on the outskirts of, or are quite detached from, the main forest area.

[1] **Adamson.** "The Woodlands of Ditcham Park, Hampshire." This JOURNAL, **9**, 1922, pp. 114–219. **Tansley.** "Early Stages of Redevelopment of Woody Vegetation on Chalk Grassland." This JOURNAL, **10**, 1923, pp. 168–177. **Tansley** and **Adamson.** "The Chalk Grasslands of the Hampshire-Sussex Border." This JOURNAL, **13**, 1925, pp. 177–223.

[2] **Watt.** "On the Ecology of British Beechwoods with special reference to their regeneration." This JOURNAL, **11**, 1923, pp. 1–48; **12**, 1924, pp. 145–204; **13**, 1925, pp. 27–73.

SOME FACTORS AFFECTING THE DEVELOPMENT OF YEW COMMUNITIES

Soil.

The soil in all the yew communities is calcareous except in the yew society above Deep Combe where the overlying friable loam is about 14 in. deep. In different parts of the valleys the soil varies from 6 in. on exposed steep slopes to 18 in. on gentler and sheltered slopes. In the valley bottoms the depth has not been determined but is no doubt much greater. No marked effect of soil in influencing the development of yew communities has been observed in the areas studied.

Wind.

All the yew-woods described, except Nos. 6–8, occupy valleys opening southwards to eastwards. Different parts of them are thus in varying degree exposed to the prevailing south-west winds, the most sheltered part varying with the lie of the valley but being generally near the valley head. That wind is a significant factor in yew-wood distribution and development is inferred from the prevalence of wind trimming among the shrubs in the near neighbourhood, from the general limitation of the yew-woods to the valleys, and from their greater and more rapid extension along sheltered slopes and to leeward of existing communities. Further, the general statement may be made here that woody vegetation first colonises the most sheltered parts of the valleys, extending thereafter to less sheltered parts.

In the three yew-woods growing on slopes the most rapid development takes place to leeward along the slope.

Rabbits.

The recent studies of Tansley and of Tansley and Adamson demonstrate the far-reaching effect on vegetation of heavy rabbit grazing. Severe grazing causes grassland degeneration and exposure of the soil, which may then be colonised by herbaceous and woody species avoided by rabbits. Even the spiny hawthorn and blackthorn are severely attacked, but the fact of greatest significance for the present study is the susceptibility of the yew. Like ash, oak and beech it requires the assistance of scrub for successful colonisation of grassland; and the efficiency of scrub for this purpose will depend upon the measure of immunity enjoyed by the scrub constituents. Of these juniper is most shunned by rabbits, and this property combined with that of wind resistance[1] gives to the juniper a significance in yew-wood establishment not possessed by any other shrub. Much importance is therefore attached to the distribution of juniper which is absent from some valleys and scarce or abundant in different parts of others—this variation in frequency influencing the structure and development of the succeeding vegetation. Adequate attention has not yet been paid to the factors governing juniper distribution but the impression is gained that juniper flourishes best on relatively shallow soils, often exposed to the prevailing winds.

[1] Watt. *L.c.* 1924, p. 159.

GENERAL DESCRIPTION OF THE VEGETATION

The phenomena described in this paper can be explained as the result of the natural processes of invasion and succession.

The difficulties confronting yew ecesis prevent effective yew colonisation of grassland. Yew, however, can invade scrub, where conditions favour its spread, and the original scrub is then ultimately suppressed. Thus yew-wood is reached through a series of intermediate stages, with or without ash, in which longevity and tolerance of shade are the chief factors in the equipment of the yew enabling it to compete successfully with its associates. Upon the death of old yews rabbit activity often prevents the regeneration of the gaps formed: hence the wood degenerates and ultimately abandons the area. Inasmuch as colonisation by scrub usually begins near the head of the valley, so this part is the first to be abandoned by the degenerating yew-wood.

In this succession from scrub to yew-wood two seres are recognised, called respectively the *juniper sere* and the *hawthorn sere* after the shrubs dominant in the initial scrub. In the hawthorn sere there are two varieties, one with ash, the other without. Briefly summarised the successions are as follows, all three sometimes contributing to the "make up" of a valley yew-wood.

Juniper sere. Scrub (juniper)→Yew scrub→Developing Yew-wood→Yew-wood.

Hawthorn sere. (*without ash*) Scrub (hawthorn)→Yew scrub→Developing Yew-wood→Yew-wood.

Hawthorn sere. (*with ash*)
↗Ash scrub↘
Scrub (hawthorn)——→ Yew-ash scrub→Yew-ashwood→Yew-wood.
↘Yew scrub↗

The juniper sere is met with on the more exposed places and, once yew invasion starts, is characterised by a relatively quick transition to pure yew-wood. The hawthorn sere begins with a scrub less efficient to protect yew and the intermediate stages are long drawn out; pure yew-wood appears late. In the succession with ash, this tree may appear before, along with, or after, effective yew invasion of scrub. This sere occurs in the sheltered parts of valleys or on the lee side of woodland. The variety without ash is found in both sheltered and partly exposed localities.

In Section I, attention is mainly directed to a study of the structure, development and fate of the yew-wood, whilst the relation of this community to other woody communities—ash-oakwood and beechwood—forms the subject-matter of Section II.

SECTION I. STRUCTURE, DEVELOPMENT AND FATE OF THE YEW-WOODS

(*a*) THE JUNIPER SERE.

The different stages of the juniper sere mostly occupy, but are not strictly confined to, exposed places (Pl. IV, Phot. 1, and Figs. 1 and 2, pp. 286–7).

Of the 22 species recorded from this sere, juniper and yew are clearly the

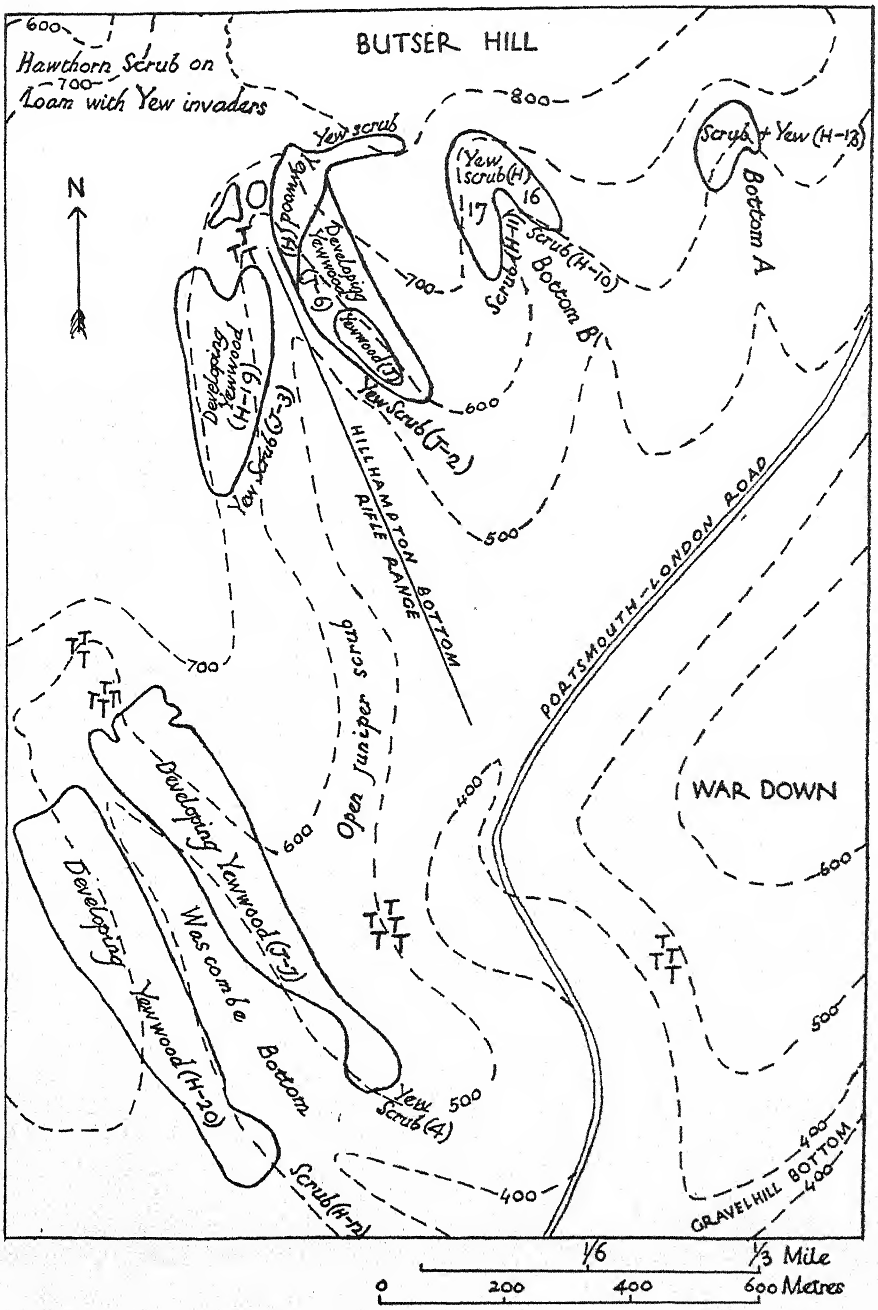


FIG. 1. Sketch-map of area south of Butser Hill showing yew-woods in the valleys. Groups of yews not in the valleys are marked TT. The woods have originated near the heads of the valleys and are moving outwards along the slopes. In Hillhampton Bottom the area first colonised is being abandoned; three old yews marked T are relicts. The whole of the head of Wascombe Bottom has been abandoned and is being recolonised by yews marked T.

main constituents: the rest are quite subordinate (list of species facing p. 304, columns 1–8)[1].

The general course of development is as follows. The juniper scrub, which at Kingley Vale consists of scattered or locally dense individuals about 3 ft.

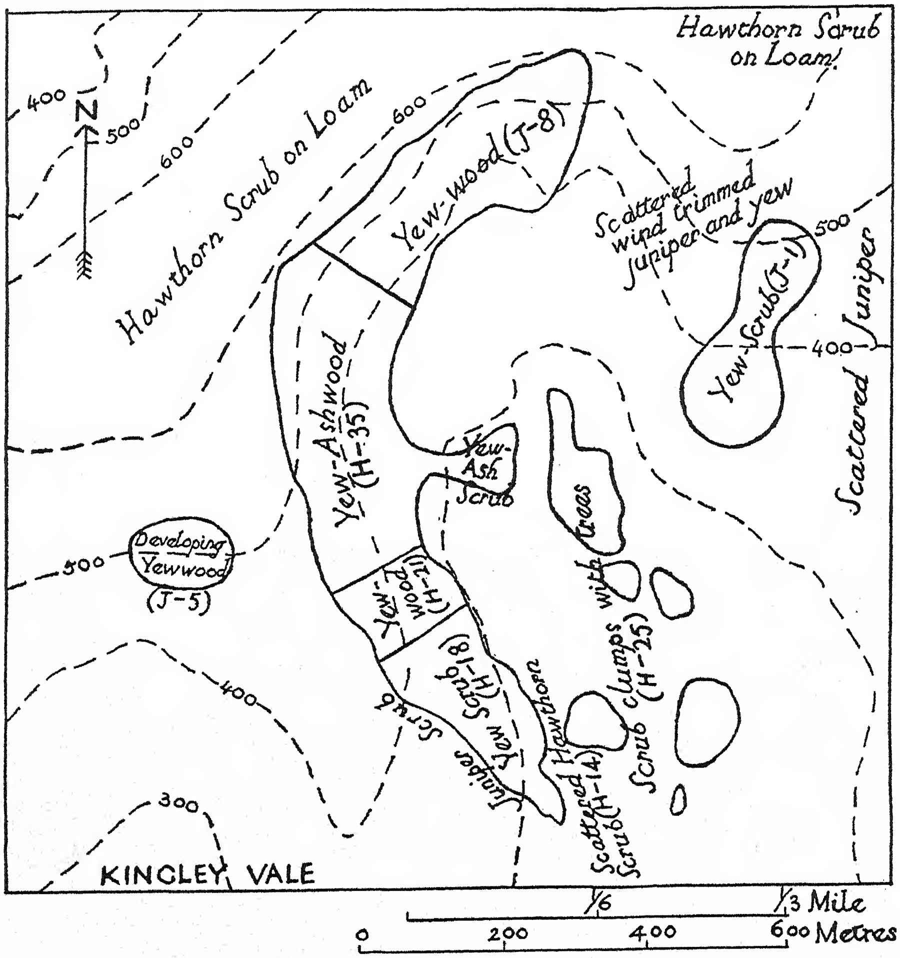


FIG. 2. Sketch-map of Kingley Vale showing development of yew-wood mainly on the slope sheltered from the prevailing south-west winds. The juniper sere (J)[1] occupies the more exposed parts, the hawthorn sere (H)[1] without ash, areas of mean exposure, and the hawthorn sere with ash the most sheltered part of the valley.

high and lopsided, is invaded by yew. Where the juniper forms the nucleus of a closed scrub yew invasion may be general, as for example on the eastern spur of Kingley Vale (Fig. 2, 1)[1] where yews from a few inches to 10 ft. are found but the majority are from 4 to 5 ft. In open juniper scrub yew invasion

[1] The reference number of the list of species (facing p. 304) corresponds with the number of the locality, given in the figures, from which the list was made. Thus J–8 means juniper sere, list 8.

is more sporadic and results in the formation of clumps consisting of yew families girt by scrub. A family consists of a central older yew with a richly branched and spreading crown (pioneer form) near which grow younger yews whose cleaner stems and lopsided crowns are due to the shading effect of the pioneer. In the scrub round the clumps small yews are growing up. This grouping of younger, straighter yews round aged pioneers is obvious in the yew scrub and developing yew-wood and can usually be made out in the pure yew-wood.

The older pioneer yew invaders show the effects of the prevailing wind but the younger yews growing up with them have mostly erect leading shoots. The sheltering effect of the yew is also seen in the improved growth of shrubs already present, e.g. juniper in the lee of a clump or in the presence of others may attain to 10 ft., a height not commonly found isolated in exposed situations. This stage in the development of yew-wood, when yew has clearly become established and is spreading, is called *yew scrub*. The most important associated species are *Cornus*, *Prunus spinosa*, *Rubus fruticosus* (agg.), *Crataegus*, *Ilex* and *Sambucus*.

The next stage, when the balance of dominance is with the yew, is called the *developing yew-wood*, which arises merely as a result of the continued increase in size of the individual yews, the enlargement of yew families and the establishment of fresh ones in the scrub between them. That this has taken place is proved by the dead remains of abundant juniper and of some hawthorn, bramble and *Clematis* found under the yews. As a result partly of the increased shelter afforded to the shrubs by the taller yews and partly by their lateral shading effect, the shrubs attain a much greater height. For example, in the developing yew-wood of the eastern slopes of Hillhampton and Wascombe Bottoms (Fig. 1, 6 and 7) the juniper has a columnar form and sometimes reaches 18–20 ft. in height. The number of species is the same as in the yew scrub and although the growth of the shrubs has improved, there is on the whole no increase in their frequency, this being prevented by the spread of the yews.

The continued growth and spread of the yew finally result in *pure yew-wood* by the suppression of the accompanying shrubs, the dead remains of these, particularly of juniper, being found on the floor. Suppression is complete on the eastern slope of Hillhampton Bottom where the yew-wood is pure, but at the head of Kingley Vale (Fig. 2, 8) occasional *Ilex* and rare straggling *Crataegus* and *Prunus spinosa* still find a place in the canopy, above which rare ash and occasional whitebeam (*Sorbus aria*) raise their crowns. The dominance of the yew is complete to a degree found in no other British tree community: the shrub layer and ground flora are absent and mosses are rare.

In this sere the yew attains a height of about 30 ft. (9 m.), with a circumference of 7 ft. 1 in. (2·12 m.) (= average of six large yews, the largest measuring

9 ft. 11 in. or 3 m.). Since the stages of the succession are completed within the life history of the yew, the size of the yews in different parts of the yew-wood may be used as evidence of the direction of spread. Applying this to the yew-wood at the head of Kingley Vale we find that the yew has invaded from the north-west corner outwards along the slope as well as up and down, but fastest along the slope and faster up than down. In this locality further movement along the slope is apparently held up, but additions to the upper and lower margins of the wood are being made from yew scrub.

The habitat is unfavourable for the establishment and growth of ash and oak, both of which are rare to occasional and mostly of poor growth; ash trees established near the bottom of the valleys show better growth but even there some suffer from wind. *Sorbus aria*, however, grows quite well and is a frequent constituent of the developing yew-woods on the eastern slopes of Hillhampton and Wascombe Bottoms.

In the yew-wood at the head of Kingley Vale one or two gaps occur, which, although not formed by the death of old yews, are of special interest for our present purpose. In some, relicts of the original scrub and grassland are found, but owing to rabbit activity on the steep slope much of the soil is bare and unstable. The following plants are found:

Atropa belladonna		Myosotis arvensis	o.
Bryonia dioica		Plantago major	o.
Sambucus nigra		Prunella vulgaris	l.f.
Arenaria serpyllifolia	l.f.	Sedum acre	r.
Cirsium palustre	l.	Urtica dioica	l.
Fragaria vesca	o.	Viola hirta	l.f.
Galium verum	o.	V. sylvatica (agg.)	o.
Lotus corniculatus	+		

In 1922 yew seedlings were recorded as frequent, but in July 1923 only one was found, the seedlings having disappeared from gaps where the light is intense enough for survival. No young yews were observed. Thus yew regeneration is effectively checked.

The effect of rabbits and wind upon the establishment and growth of juniper and yew are clearly demonstrated in the woody vegetation colonising the wind-swept slope of the steep eastern spur of Kingley Vale (Pl. IV, Phot. 1, and Fig. 2). Here the scrub is open and consists solely of yew and juniper, the other shrubs being apparently unable to grow here. Both plants are wind-trimmed and in greater degree towards the north-east corner of the Vale. The juniper probably suffers more than the yew, for in the most wind-swept corner scattered, lopsided yews are found with no living, and rare or occasional dead juniper.

Almost every yew is growing along with a living or a dead juniper. Most of the yews are small—12–18 in. (30–45 cm.) high, often very small—4–7 in. (10–18 cm.), are closely nibbled, conical in shape and old. A small yew 7 in. (18 cm.) high showed approximately 55 growth rings.

The inference to be drawn from this and the previous observation is that

yew and juniper are the most wind-resistant elements of scrub and that successful establishment of yew in grassland is conditioned by the presence of scrub protective against grazing animals. At the same time it may be questioned if the yew seedling can readily become established in a grassy turf, and its association with scrub elements may, in the first instance, be due to the provision round the bases of shrubs of suitable germination and establishment conditions, such as exposed soil or shade. Experimental proof is lacking, but the record of one seedling only from an enclosure made eleven years earlier and near to abundant yews strengthens the suggestion. This seedling, too, was found in the "deep shade of *Crataegus*"[1]; according to some observers the yew seedling is intolerant of strong illumination[2].

The conclusion that protective scrub is necessary for successful establishment of the yew is supported by observations from the juniper scrub in other parts of Kingley Vale, where the observed facts are similar to those just described: from the association of yew with *Crataegus* and *Prunus spinosa* at Stead Combe; with *Prunus* in Bottom "A," with juniper in Hillhampton and Wascombe Bottoms; and by the occurrence of inadequately protected and heavily grazed yews in all these localities[3]. Of the scrub elements, juniper is apparently the most effective to protect yew, and this is reflected in the more rapid colonisation of juniper scrub than of hawthorn scrub. This effective initial invasion means a rapid passage to yew-wood.

The view that yews are immune from attack by grazing animals is erroneous, for these small conical yews are trimmed down by such animals, probably by sheep, hares and rabbits. Rabbits also nibble the bark off stems and branches. Lowe[4] states that "deer, sheep, goats, hares and rabbits eat yew without harm" and Elwes[5] records that he has seen yew stems gnawed by rabbits.

The transition from the juniper to the hawthorn sere is recognised by the increasing frequency of *Crataegus* and a corresponding decrease in juniper. List 4 from the eastern slope of Wascombe Bottom indicates a transitional community. Here and in the more sheltered parts of the other localities juniper grows larger, and taller, has often a spreading habit and bears pale sickly foliage in contrast to the healthy appearance of large or small junipers in exposed communities. The physiological cause of this is unknown but soil factors evidently contribute to the production of the effect.

(*b*) The Hawthorn Sere.

This sere occupies the less exposed parts of the valleys. The difference in the habitat is reflected in the flora, for in the juniper sere there are only 22 species, while in the hawthorn sere there is almost twice that number—42.

1 **Tansley.** *L.c.* 1923, p. 176.
2 **Hempel** and **Wilhelm.** *Die Bäume und Sträucher des Waldes*, 1893, p. 200.
3 But see also p. 302.
4 *Yew-trees of Great Britain and Ireland*, 1897, p. 150.
5 **Elwes** and **Henry.** *Trees of Great Britain and Ireland*, 1906, **1**, p. 119.

Of the 20 additional, most are local or have a low frequency. These, it is interesting to note, include *Ruscus aculeatus* which was not observed in exposed places: the evergreen *Ilex* is however equally widespread in both.

The two varieties of the hawthorn sere are separated on the basis of the presence or absence (or rarity) of ash. Floristically the two are similar, the sere without ash containing 35 species, the sere with ash 39. There are seven—*Acer campestre, Calluna vulgaris, Rubus idaeus, Ruscus aculeatus, Salix caprea, Ulex europaeus, Viburnum opulus*—not recorded from the sere without ash, whilst there are three—*Humulus lupulus, Pinus silvestris* (subspontaneous), *Prunus insititia*—not recorded from the sere with ash. All these species play a minor part in the vegetation in which the dominants are the same. Apart from the variation in the frequency of ash, the main difference is found in the relative frequency of the species common to both; *Clematis, Cornus* and *Rubus fruticosus* (agg.) are more frequent and *Ilex* more evenly distributed in the sere with ash, whilst *Prunus spinosa* is more frequent and *Rhamnus* more widespread in the sere without ash.

The Hawthorn Sere without Ash.

On the whole, the variety without ash is more exposed than the variety with ash. Exceptions occur; for example, the yew communities on the sheltered western slopes of Bottom "B," Hillhampton and Wascombe Bottoms; and exactly why ash is scarce in, or absent from these localities is not understood.

In the development from scrub to yew-wood the same stages are recognised as in the juniper sere and the process of invasion and succession is similar; only the differences need be emphasised here. The species are listed in columns 9–21.

The chief constituents of the scrub, *Crataegus* and *Prunus spinosa*, are accompanied by a number of shrubs whose frequency varies much in different localities. In the Butser Hill examples there are only 15 species, all, except the dominants and yew and elder, with a low frequency, but in Stead Combe (Fig. 3, 9) and Kingley Vale (Fig. 2, 14) there are 25 species including many of the commoner "chalk" scrub elements, some with a high frequency—*Euonymus* (f.), *Ligustrum* (a.), *Rosa micrantha* (f.). A similar difference is noted between the richness of yew scrub from Holt Down (Fig. 4, 15) and Kingley Vale (Fig. 2, 18) (29 species) and the poverty of the same stage from Butser Hill (14 species). These differences are emphasised by the accompanying grassland which near the Butser Hill examples contains much less *Poterium sanguisorba* than in the other localities, where this species is conspicuous. The probability is thus indicated that the present grouping includes habitats whose soils are really different.

The association of yew and hawthorn in this sere is much less common than that of yew and juniper in the juniper sere. This is due to the lesser ability of the hawthorn to shield invading yews so that not only are yew

families fewer in number but they enlarge much more slowly. That they are progressive is shown by the dead remains of *Crataegus*, *Clematis* and *Rubus fruticosus* (agg.) found under the yews. Thus yew scrub and the developing yew-wood belonging to the hawthorn sere are much opener than the corresponding stages of the juniper sere, the large and small yew families being separated by gaps, which, in rabbit-infested areas, bear a scattered scrub, a crisp turf, rabbit-immune herbs or no vegetation at all. The establishment

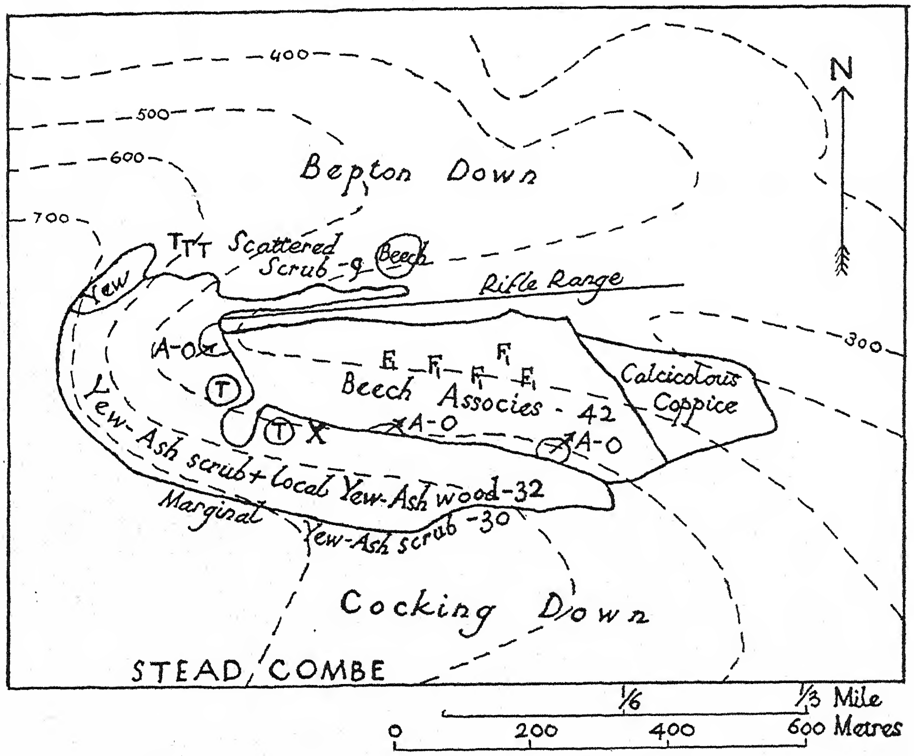


FIG. 3. Sketch-map of Stead Combe showing distribution of the "yew system" and the "beech system." A very old yew grows in the position marked X; pure yew-wood is local marked T. Five old pioneer beeches grow in the positions marked F_1. The ash-oak associes has been almost entirely obliterated by the beech associes advancing up the slope; patches (A–O) remain.

of fresh yew families is therefore difficult and the approximation of the existing ones slow. Locally this may not be true, as for example in a large patch of "thicket" yew scrub on the eastern slope of Bottom "B," nor does it hold good generally of the yew scrub in Kingley Vale. This, however, is derived on its western side from juniper scrub and on the valley side from slowly fusing scrub clumps, and here the intervals between the yews contain a rich scrub. The general openness referred to is not observed in the final stage but the two examples from Kingley Vale (Fig. 2, 21) and Hillhampton

Bottom are of small extent and do not upset the conclusion based on the study of the preceding stages that the passage from scrub to yew-wood is typically much slower in the hawthorn than in the juniper sere.

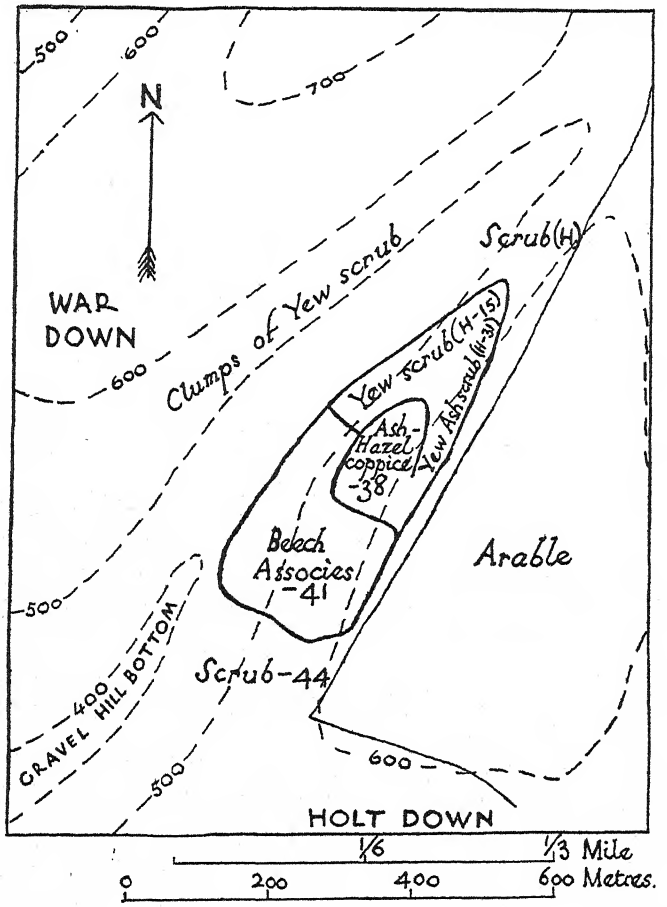


FIG. 4. Sketch-map of woodland on Holt Down, showing the distribution of the "yew system" and the "beech system." In the "yew system" ash grows only on the lee side. The ash-oak associes of the beech system is represented by ash-hazel coppice.

Changes in form and frequency accompany increasing shelter. Exposed and isolated blackthorn, hawthorn and yew are lopsided; in scrub, hawthorn frequency increases in clumps nearer the yew scrub, and in the yew scrub near the head of Bottom "B" attains a height of 25 ft. The frequency of *Clematis*, *Cornus* and *Rhamnus* is also greater in yew scrub and developing yew-wood than in scrub.

At the most, ash and oak are occasional and small except in one locality where ash is locally frequent. This is the northern margin of the developing yew-wood on the western slope of Hillhampton Bottom. Beech is recorded

only from the Stead Combe scrub where it grows isolated and in families, demonstrating the rapid transition from scrub to beechwood in exposed places[1].

In the yew scrub of Bottom "B," where there are no trees apart from the yew, there grows a patch of *Mercurialis perennis*.

The severe rabbit pressure is demonstrated in the Butser Hill examples by the large areas of bare soil with a mobile rubble of chalk stones and flints, by patches of short grassy turf, and by the replacement of grassland by an assemblage of plants disliked by rabbits—*Senecio jacobaea*, *Cirsium lanceolatum*, *Urtica dioica*, *Teucrium scorodonia*, *Myosotis arvensis*[2]. In addition, small (7–9 in.) heavily grazed bushy yews are found, and the shoots of *Crataegus* and *Prunus spinosa* are cut off. In this way beds of low-growing decrepit *Prunus spinosa* are formed. The activity of rabbits is not limited to shoots accessible from the ground but is pursued into the crowns of taller bushes (3–4 ft.), where the upper sides of branches are barked and young erect shoots cut across. This results in a flat or convex crown which can extend laterally but not, or very slowly, upwards. A keeper informed me that this was the work of rabbits during the winter months when food is scarce, but in September I collected fresh shoots lying on the ground below the bushes. Both *Prunus spinosa* and *Crataegus* are attacked in this way.

In this sere *Sambucus* is locally common, growing abundantly on loose soil cast up round rabbit burrows and fairly frequently on soils exposed by severe rabbit grazing: its unusual frequency in the examples from Butser Hill is correlated with heavy rabbit pressure. Although apparently immune to rabbit attack, *Sambucus* seems to have little power to extend or persist, and this localisation is probably connected with the requirements of seed germination and seedling establishment, because the absence of *Sambucus* from grassland cannot be attributed to rabbit activity. And the same may hold good for some of the herbs which replace degenerate grassland.

In these rabbit-infested areas attempts to colonise gaps by woody species other than *Sambucus* are largely frustrated, so that the openness of yew scrub and developing yew-wood and the slow fusion of yew families are readily understood. It is doubtful if under present conditions large areas of continuous pure yew-wood could be formed.

In the pure yew-wood in the north-east corner of Hillhampton Bottom the yew attains a height of 40 ft., and the average girth of six large yews is 8 ft. 3 in. (2·5 m.)—the largest measures 9 ft. 2 in. (2·75 m.). As in the juniper sere, the largest yews in the valleys grow at the head of the valley or in that part of the community nearest to it; the size decreases outwards along the slope. Thus the direction of movement along the slopes, indicated by the order of the developing communities is confirmed by the age of the yews.

[1] **Watt.** 1924, p. 182.

[2] For a fuller account of this kind of vegetation, see **Tansley** and **Adamson.** *L.c.* 1925, pp. 211–218.

At the head of Bottom "B" large gaps, occupied by turf, by rabbit-immune herbs and by a large colony of *Sambucus,* separate members of an apparently decadent scrub of hawthorn, sloe and yew.

The Hawthorn Sere with Ash.

In this sere the normal course of development to yew-wood is not interrupted by the entrance and subsequent elimination of ash; its presence merely delays the appearance of pure yew-wood. The following stages are recognised: scrub, yew scrub, ash scrub, yew-ash scrub, yew-ashwood, yew-wood.

These stages are identified from the most sheltered parts of Stead Combe (Fig. 3) and Kingley Vale (Fig. 2) and from the three slopes Downley Brow (Fig. 5), Chilgrove Hill (Fig. 6) and Holt Down (Fig. 4), where development takes place mainly away from the direction of the prevailing winds. Wind and rabbit activity are apparently the chief factors limiting the distribution of scrub, which is found best developed to leeward of the Downley Brow and Holt Down woodlands. In the similar position on Chilgrove Hill rabbit activity has denuded the narrow strip of steep slope between the woodland and an abandoned chalk pit now being colonised by a rich scrub. In the grassland of the lower slopes colonisation by woody plants is extremely difficult, as the work of Tansley on Downley Brow proves, so that the scrub forms a discontinuous fringe to the lower side of the woodland strips of Downley Brow (Fig. 5, 28) and Chilgrove Hill and along the upper exposed margin of Stead Combe (Fig. 3, 30). In Stead Combe this marginal scrub widens out on the more sheltered gently sloping and east facing part of Cocking Down, and along the upper margin of Downley Brow (Fig. 5, 29) and Chilgrove Hill (Fig. 6, 27) the scrub forms a continuous and wider zone. In the grassland of the lower slope of Chilgrove Hill (Fig. 6, 26) and in the valley bottom of Kingley Vale (Fig. 2, 25) scrub clumps of varying size and with or without trees are found.

The extent of the scrub sets limits to the successful establishment and spread of both ash and yew: young ash is indeed locally abundant in the grassland but is kept down by persistent grazing, and isolated yews suffer in the same way. Of these two trees, ash is the more mobile so that where scrub is extensive and conditions suitable ash colonisation precedes that of yew. This is exemplified on Downley Brow (Fig. 5, 24) and Chilgrove Hill (Fig. 6, 23) where an ash scrub stage precedes effective yew colonisation. On Holt Down, probably because of exposure rendering ash establishment difficult, yew scrub precedes the stage with ash, which even then appears on the lee side only (Fig. 4, 15 and 31).

On the other hand, where the scrub is of small extent and its spread extremely slow, as in the narrow fringing scrub and in the scrub clumps, no such fractional separation of the stages can take place and scrub passes

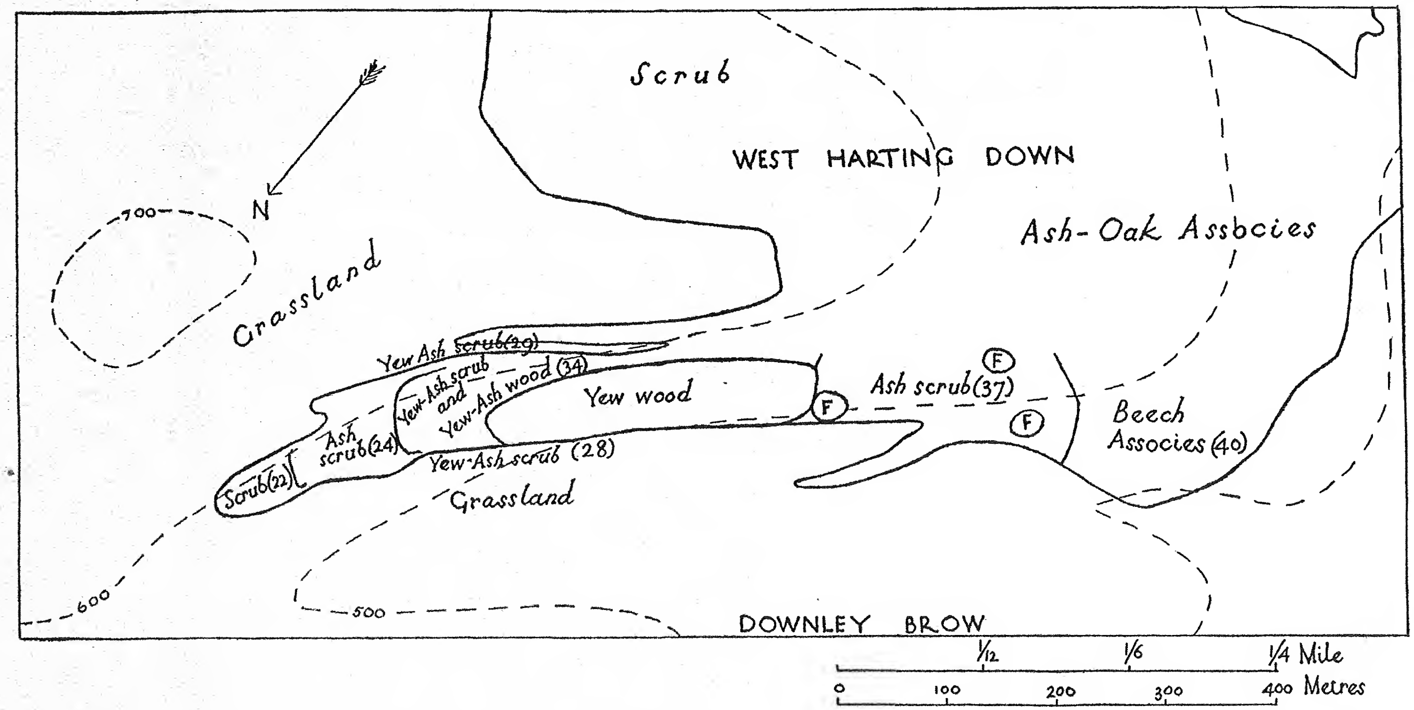


FIG. 5. Sketch-map of woodland on Downley Brow showing the seral stages in the development of yew-wood, and ash scrub and the beech associes of the beech system. Development is mainly to leeward. In the ash scrub occur degenerating groups (*F*) of old pioneer beeches. The beech system is continuous with the ash-oak associes (sere 3) of the plateau.

directly to yew-ash scrub. The effect is seen in the abrupt transition from grassland through a narrow zone of yew-ash scrub to a later stage with old yews and in the structure of scrub clumps consisting of yews encircled by a narrow scrub colonised by ash. That the rate of enlargement of some of these clumps is extremely slow is evidenced from the very large and old yews, the average girth of eight large trees being 14 ft. 8 in. (4·47 m.)—maximum 21 ft. 0 in. (6·4 m.). These still border on grassland or are hugged by a narrow scrub. Some of the larger clumps at Kingley Vale show development towards true woodland structure which is attained in certain clumps at Chilgrove, where there is a canopy of ash, a definite shrub layer, and a ground flora

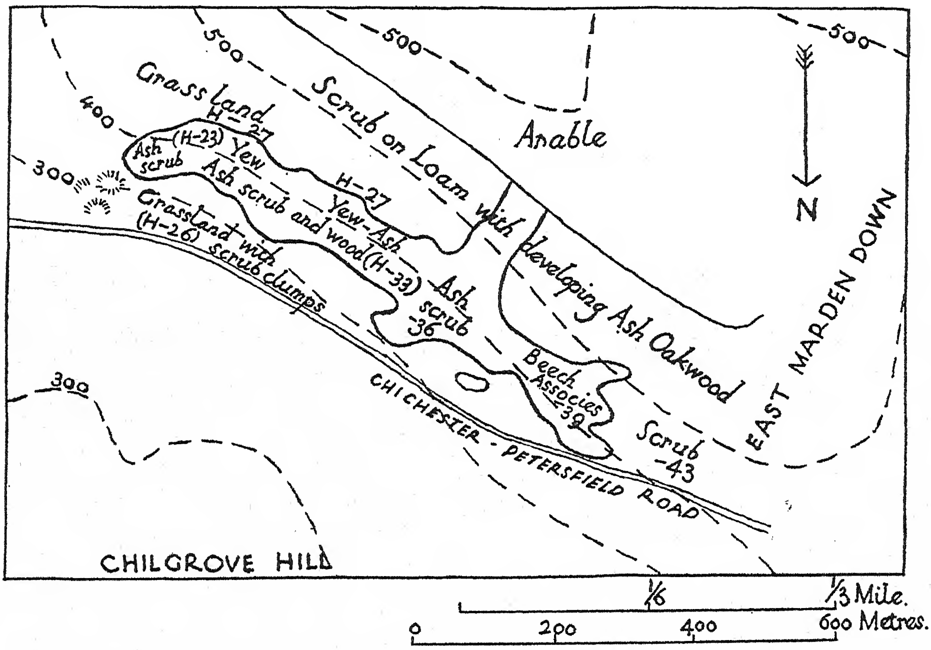


FIG. 6. Sketch-map of woodland on Chilgrove Hill showing similar distribution of stages found on Downley Brow.

dominated by *Mercurialis*. The zone of scrub along the upper margin of the Downley and Chilgrove woods is freely invaded by ash and yew but is too narrow to permit a separation of the ash scrub and yew-ash scrub stages, although ash is decidedly more frequent than yew along the forward margin.

The ash scrub consists of a hawthorn scrub freely invaded by ash which forms the canopy. The tangles of dead *Clematis*, *Crataegus* and *Rubus fruticosus* (agg.) indicate the change from open conditions to growth under canopy and demonstrate this ash scrub to be the early stage in the development of the ash-oak associes preceding beechwood[1]. The only woodland herb is *Mercurialis* which is occasional to locally frequent, but no true ashwood with

[1] Watt. *L.c.* 1924, p. 164.

shade forms of *Crataegus* and with a woodland flora is found. This is prevented by the establishment and spread of the yew in the ash scrub, thus giving rise to the yew-ash scrub. Here, by the establishment and growth of young yews, and by the enlargement of existing yew families, the scrub is gradually suppressed, but the taller ash survives. The rate of development varies much. At Downley and Chilgrove the ash scrub is effectively colonised by yew which quickly suppresses the scrub, but at Stead Combe, where the yew-ash scrub (Fig. 3, 32) is extensive, the process is a slow one. This is apparently correlated with the openness of the hawthorn scrub, in which diffuse yew families and scattered yews occur. Here, too, there is a woodland flora dominated by *Mercurialis perennis*.

In the yew-ashwood most of the scrub has been suppressed, and the wood consists essentially of an upper diffuse canopy of ash and a lower of yew. This stage is identified from Stead Combe, Chilgrove (Fig. 6, 33) and Downley (Fig. 5, 34), but is best represented at Kingley Vale (Fig. 2, 35), where the yew-ashwood occupies the whole of the north-west corner.

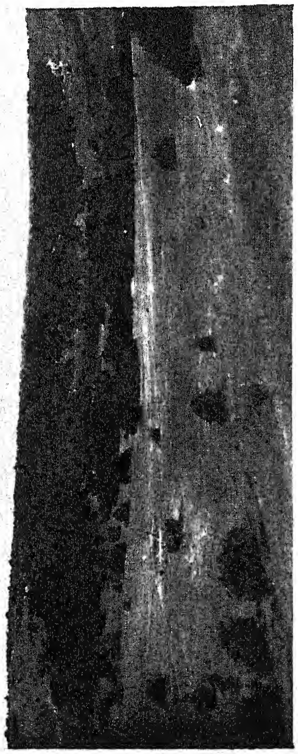
The ash attains a height of 50–60 ft. (15–18 m.) and a diameter of a foot or more; some old stems lie rotting on the floor. The yews are of large and imposing size, up to 40–50 ft. (12–15 m.) in height and to 18 ft. 6 in. (5·64 m.) in basal girth—the average of 17 large trees at Kingley Vale being 13 ft. 2 in. (4 m.). By the death of some old yews gaps occur whose flora is described later (see p. 300).

The Kingley Vale yew-ashwood affords an excellent illustration of the extreme slowness of the fusion of yew families, for in the lower part of this wood relicts of the original scrub still survive between yews considered by Lowe to be 500 years old[1]. In the upper and younger part of the wood the development has been much more rapid.

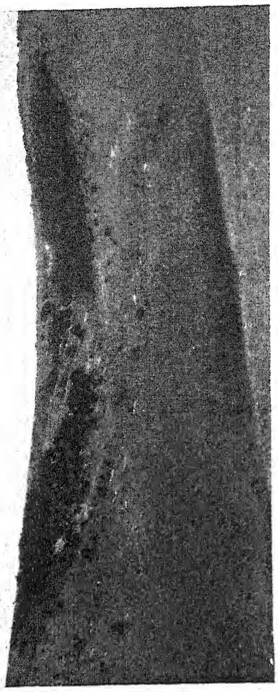
When the ash trees die, their replacement by young growth is prohibited by the shade of the yews; yew-ashwood passes to yew-wood. This appears locally in Stead Combe but is best developed on Downley Brow, where the canopy is almost pure. The derivation of the yew-wood from the approximation and fusion of yew families is evident from the arrangement of the smaller straight-stemmed yews round the larger pioneer forms; from the association of the surviving ash with the smaller yews; from the dead ash and hawthorn on the floor; and from the relicts of scrub in small enclaves.

The direction of spread is confirmed from examination of the size of the yews in different stages and in different parts of the same stage On Chilgrove Hill, Holt Down and Downley Brow the size of the yew increases from the early stages to the last stage reached in the different localities; at Kingley Vale the oldest yews are found nearer the foot of the slope, and at Stead Combe the oldest yews, including one with a basal girth of 19 ft. 9 in. (6 m.), grow near the boundary between the yew community above and the beech-

[1] *L.c.* p. 60.



Phot. 1. General view of Kingley Vale, looking up the valley.



Phot. 3. General view of Hillhampton Bottom, showing yew-woods on the slopes and the yew relicts in the abandoned area near the head of the valley.

Phot. A. G. Tansley, April 1921

Phot. 2. General view of combes on Butser Hill, showing limitation of yew-woods to valleys. Starting from the right, Bottom "A," Bottom "B" and Hillhampton Bottom.

[Adamson, 1922, Pl. X, Fig. 3.]

Phot. A. G. Tansley, April 1921

Phot. 4. Head of Hillhampton Bottom: in the foreground, part of the abandoned area; in the centre, two ash trees in yew-ash scrub clumps; on the sky line, hawthorn scrub with yew invaders on loam.

[Adamson, 1922, Pl. X, Fig. 2.]

wood below, in the position marked X in Fig. 3. In all these invasion has taken place outwards from the oldest yews; faster along the slopes than up and down and faster up than down; in the valley bottoms faster up than down.

While ash, oak and beech are unable to grow under a yew canopy, they may colonise the intervals between yew families in the developing yew society and may become locally dominant there. In this last case development may proceed to maturity, when the colony exhibits true woodland structure and is to be considered an outlier of woodland. The relation of the yew to these will be considered in the next section. Meantime attention is directed to isolated trees or groups of trees which form patches of developing woodland within the developing yew society.

Two facts are relevant here: the longevity of the yew and its dependence on scrub. So long as scrub grows in the intervals between yew families the yew can colonise readily and gradually fill up the gap. This process is well illustrated in the development from scrub to yew-wood just described, in which the long-lived yew utilises and then suppresses the scrub of the ash scrub and then outlasts the ash. In this way pure yew-wood is formed. The same may apply also to oak although oak is rarely found in the developing yew-woods. With beech the case is different, especially if it has a pioneer form and grows in groups, as for example at Chilgrove and Stead Combe. The shade cast by the beech kills out the scrub and hinders yew colonisation and even if yew does become established the saplings often die or show poor growth and few leaves. It is doubtful if this colonisation is really effective. The beech is unable to regenerate and the surrounding long-lived yews still survive when by the death of the old beeches a gap is formed. This will not usually be occupied by the yew until scrub first becomes established. Groups of beech may in this way hinder the development to pure yew-wood.

THE DEVELOPMENT OF WOODY VEGETATION IN THE VALLEYS.

A separation between the seres has been made to trace the development of the different kinds of vegetation, but it has been shown that the two hawthorn seres and the juniper sere may contribute to the formation of a valley yew-wood; all three types of sere contribute to the yew-wood of Kingley Vale.

Photographs 1 and 2 (Pl. IV) show the striking limitation of the yew-woods to the valleys. This is due to the absence of scrub in the adjoining plateau grassland, but where the soil is deeper with superficial loamy deposits a hawthorn scrub is found, in which yew readily becomes established (see Pl. IV, Phot. 1 and 4, Figs. 1 and 2). In the bottoms of narrow valleys scrub and yews are absent owing to the intense rabbit grazing there.

From a study of the ages of the yews in the valleys as a whole it is found that the oldest yews grow near the head of the valley in the part most sheltered from the prevailing winds and that the age decreases outwards with distance from this point. This is true of all the valleys. It is thus believed that yew

colonisation first began here in a scrub of the hawthorn type and spread outwards, the scrub forming an advancing zone under the shelter of the progressing yew-wood and changing its character as the environment changed; in the more exposed parts hawthorn scrub is replaced by juniper scrub.

Juniper scrub may form a separate centre for yew invasion, as on the eastern spur of Kingley Vale and on the eastern slope of Hillhampton Bottom, where, locally, development has proceeded through yew scrub, developing yew-wood to pure yew-wood. At Hillhampton Bottom the interval between this outlier and the yew-wood in the north-east corner has been occupied by a juniper scrub which has succeeded rapidly to developing yew-wood by the free invasion of yew.

In any one sere the oldest yews are found in the most advanced stage represented in a valley, and not in the most advanced stage of development represented irrespective of sere. Thus the yew-ashwood at Kingley Vale contains the oldest yews on the slopes but it is flanked by pure yew-woods which, although distinctly younger, have nevertheless attained the final stage in their respective seres.

It is where the yews are oldest that degeneration begins.

Degeneration of Yew-woods.

Three stages in the process may be described: failure to recolonise gaps formed by the death of old yews; disappearance of the yew-wood except for some relicts; abandonment of the area.

The difficulties attending the colonisation of primary gaps by yew and ash have already been pointed out and the same is true of gaps formed by the death of old yews. This is best illustrated in the yew-ashwood at Kingley Vale where a snowstorm in the winter of 1913–14 is reported by Mr Collie, the late forester at Goodwood, to have caused much damage, uprooting large and some small yews and breaking the branches of old standing trees. The gaps formed are bare or are colonised by a flora of special interest. The following are the species recorded from 13 gaps:

Atropa belladonna in 5 gaps
" " seedlings l.a.
Bryonia dioica in 4 gaps
Cornus sanguinea in 1 gap
Clematis vitalba seedlings in 3 gaps
Fraxinus excelsior, one- and two-year seedlings
" " two young plants in 1 gap
Ilex aquifolium in 2 gaps
Taxus baccata, one seedling
" " one plant 6 in. high, nibbled
Sambucus nigra in all 13 gaps

Carex glauca	+
Cirsium palustre	+
Fragaria vesca	o.—l.f.
Myosotis arvensis	o.
Mercurialis perennis	l.d.
Prunella vulgaris	o.
Senecio jacobaea	o.
Sonchus oleraceus (seedlings)	l.f.
Urtica dioica	l.d.
Verbascum nigrum	+
Veronica chamaedrys	o.
Viola hirta	o.
V. silvatica (agg.)	o.—l.f.

Mosses are well represented in species but have difficulty in maintaining a foothold owing to rabbit activity.

The list shows that neither ash nor yew is successfully colonising the gaps formed. Only two ash plants older than 2 years were found, the majority of seedling ash being eaten by rabbits, as were also the yews, one of which, growing up in the fork of a superficial branched root, had temporary protection but is now closely nibbled. There is no establishment of a scrub fit to protect the seedlings; only the relatively immune *Bryonia*, *Atropa* and *Sambucus* being at all well represented. *Sambucus* is present in all the gaps and dominant in some.

There is an abundance of yew seeds on the floor of the wood, but the vast majority are without kernels. Some of the seeds have been split into two equal halves, but many have holes with ragged edges cut in them. The seeds are believed to be split by tits and the ragged holes made by mice[1], but both observations lack experimental verification.

The beginnings of degeneration at the head of Bottom "B" are demonstrated by the large gaps occupied by abundant *Sambucus* and rabbit-immune herbs; a later stage is seen at the head of Hillhampton Bottom (Pl. IV, Phot. 3 and 4, Fig. 1). This area is heavily rabbit-grazed. Herbs avoided by rabbits predominate, but on part of the western slope these are replaced by a crisp grassland over which loose chalk rubble is slipping down the slope. The woody vegetation is represented by two groups of clumps separated by a zone almost without woody plants. These groups adjoin the woods of the eastern and western slopes respectively. In both cases the clumps are dominated by yew families accompanied by a scrub of the hawthorn type. Some of the clumps are progressive as the dead remains of scrub under the yews show, although enlargement of the clumps is slow; but some families are without effective scrub elements and fail to extend. Some yew families indeed are represented by isolated old yews clear of branches 4–8 ft. up. In the clumps the oldest yews are of pioneer form and large size (the largest measuring 10 ft. 7 in. in girth). It is worthy of note that ash grows here, and in the adjoining developing yew-wood on the western slope this tree is confined to the zone next to the clumps just described.

Between the two groups of clumps lies the area of closely nibbled grassland in which grow one isolated hawthorn, two isolated sloes and three old yews. These yews are near the foot of the slope and girth 6 ft. 3 in., 7 ft. 3 in., and 9 ft. 0 in. The last two are clear of branches from 4–9 ft. up and on the first, large branches begin at 6 ft., but small epicormic branches grow out below (Pl. IV, Phot. 3, Fig. 1).

These three old yews as well as the isolated old yews near the developing yew-wood are considered to be the survivors of a community with yew and ash, which once occupied this part of the valley, the present distribution of ash marking the former bounds of this community.

[1] But see also **Kirchner, Loew** and **Schröter**. *Lebensgeschichte der Blütenpflanzen Mitteleuropas*, **1**, 1908, p. 77.

In addition to these detached yew clumps and large isolated yews bordering the northern margin of the yew-wood, developing clumps with young yews and isolated yews about 1 ft. in diameter, 10 ft. high and branched to the base grow on the western slope. These are considered as pioneers recolonising the abandoned area.

On the western slope of Hillhampton Bottom the oldest yews border on the area now almost abandoned, but in the woods of both slopes of Wascombe Bottom the oldest yews grow near, but not on, the north-west margin and are separated from the abandoned area by a narrow belt of almost continuous yew contiguous with the main body.

At the head of Wascombe the vegetation consists mainly of herbs avoided by rabbits. On the western part two areas of grassland with much moss are found, one adjoining the yew-wood the other on the slope of the western arm of the bifurcating valley head. Woody plants are represented by the following:

Atropa belladonna	l.f.	Sorbus aria	r.
Bryonia dioica	o.	Rhamnus catharticus	o.
Cornus sanguinea	l.	Rubus fruticosus (agg.) dead	r.
Crataegus monogyna	o.—f.	Sambucus nigra	f.—l.d.
Prunus spinosa	o.	Taxus baccata	f.

These are found singly or in clumps: the larger clumps consist mainly of *Sambucus*. Many of the hawthorn bushes are old and thick-stemmed and the decrepit sloe is pruned by rabbits.

Taxus may grow singly or in company with *Rubus*, *Crataegus* and *Rhamnus* or may form small families. The yews vary in height from 1 to 20 ft., and are of pioneer form, branched from the ground. The diameters of the two largest were estimated at 21–24 in. It is of interest to note that on the eastern slope and just outside the yew-wood there grow within a radius of about 20 yds. nine young yews from 12 to 18 in. high—all untouched by rabbits.

Complete abandonment of the head of the valley and a later stage in recolonisation are demonstrated in Wascombe Bottom (Pl. V, Phot. 5, and Fig. 1, p. 286). The only evidence that yew-wood once occupied the head of the valley is that the oldest yews grow near the north-west margin and that general progression of the woody vegetation is south-eastward along the slope. Direct evidence has disappeared with the complete disappearance of the original community.

It is of interest to observe here that Bottom "B," Hillhampton Bottom and Wascombe Bottom demonstrate a series in yew-wood degeneration, which is probably related to the size of the valleys. For it is likely that the longer and more sheltered valley of Wascombe would be first colonised and the yew-wood develop earlier than in the smaller bottoms. These in turn show yew-woods in descending order of development—Hillhampton, "B" and "A" Bottoms.

The conclusion that the yew-wood has abandoned the head of the valley is supported by the distribution of the yews in the neighbourhood of Deep Combe and Malcombe (*v.* Fig. 7). Reference to the figure will show that the

Phot. 5. Head of Wascombe Bottom, showing part of the rabbit-devastated area abandoned by yew-wood. On the right appear yews recolonising the area.

[Tansley and Adamson, 1925, Pl. VI, Phot. 3.]

Phot. 6. Holt Down, showing open hawthorn scrub with yew invaders south of the beech associes.

[Tansley, *Types of British Vegetation*, Pl. XVIII *b*.]

WATT—YEW COMMUNITIES OF THE SOUTH DOWNS

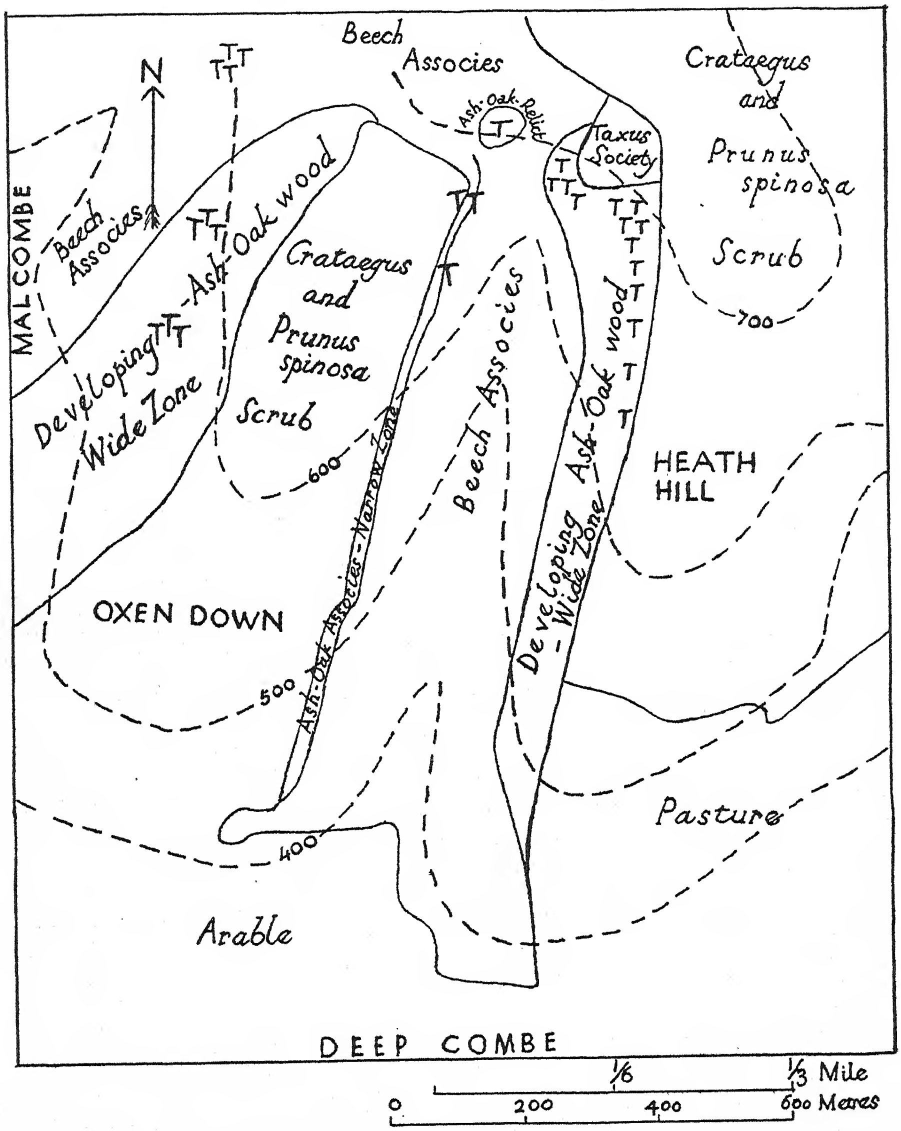


FIG. 7. Sketch-map showing distribution of woody vegetation round Deep Combe. The yew community has moved out from the valley, mainly eastwards and north-eastwards, and is now represented by the yew society and by abundant yews to the south of it in the forward zone of the ash-oak associes. The abandoned valley is now occupied by the beech system. Similar relations hold good in the adjoining valley of Malcombe.

yews occur round and above the head of Deep Combe and that the bulk of them are found eastwards of the valley. North-eastwards lies a *Taxus* society[1]: elsewhere the yews are mostly scattered although patches of locally dominant yews are found. The structure of this society indicates progression eastwards. On the east and north-east margin the yew community is in the yew scrub stage with some older pioneers but many young yews. The average height is from 15–20 ft., and the average girth of 27 stems is 23 in. (extremes 13 in. and 48 in.). Behind, the yews stand less densely upon the ground and an easy passage can be made under the higher and closed canopy; the average girth of 29 stems is 34 in. (extremes 9 in. and 8 ft. 8 in.). In the ash-oakwood behind there is one yew family but the yews are mostly scattered; the tallest are from 35 to 40 ft., and the average girth of 29 stems is 48 in. (extremes 11 in. and 8 ft. 10 in.).

The distribution of the yews in the adjoining valley of Malcombe corresponds closely with that for Deep Combe. There is, however, no yew society although patches of locally dominant yew are found in the ash-oak associes east of the valley.

The evidence from Deep Combe shows that the *Taxus* community is migrating outwards from the valley—the main body travelling eastwards and north-eastwards. Here the abandoned area has been occupied by woodlands which have developed from scrub to ash-oakwood and beechwood.

Summary of Section I.

In this section the structure and development of several yew-woods on the South Downs are described, and evidence brought forward to show that these are migratory.

The yew meets with considerable difficulty in establishing itself in grassland. Perhaps ecesis in a grassy turf is difficult but the prevalence of closely nibbled isolated yews and the frequent association of yews with prickly shrubs suggest the efficacy of the animal factor in preventing successful yew invasion of grassland. This suggestion is supported by the close parallel between the degrees of susceptibility of prickly scrub elements to rabbit attack and the efficiency of these elements in promoting yew colonisation. Juniper is least attacked by rabbits and the association of juniper and yew is the most frequent. Hawthorn comes next in importance. For successful yew colonisation of grassland, scrub is essential.

The conclusion come to in a previous work that juniper and yew are the most wind-resistant of scrub elements is supported by the observations recorded here: hawthorn scrub is best developed in the most sheltered parts of valleys whilst a juniper scrub may be present on the exposed slopes as well as on sheltered slopes.

Two seres are recognised: a juniper sere and a hawthorn sere. Both culminate in pure yew-wood, but in the juniper sere the passage from scrub

[1] Watt. *L.c.* 1924, p. 167.

	Juniper Sere														Hawthorn Sere (without ash)		
Reference Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Community	Yew scrub				Developing yew-wood			Yew-wood	Scrub							Yew scrub	
Locality	Kingley Vale	Hill-hampton Bottom (eastern slope)	Hill-hampton Bottom (western slope)	Wascombe Bottom (eastern slope)	Kingley Vale	Hill-hampton Bottom (eastern slope)	Wascombe Bottom (eastern slope)	Kingley Vale	Stead Combe (northern slope)	Bottom "B" (eastern slope)	Bottom "B" (western slope)	Wascombe Bottom (western slope)	Bottom "A"	Kingley Vale (valley floor)	Holt Down	Bottom "B" (eastern slope)	Bottom "B" (western slope)
Acer campestre	.	.	.	.	r.	.	.	.	.	.	.	.	.	.	.	.	.
A. pseudoplatanus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r.	.	.
Atropa belladonna	.	r.	o.	.	.	.	.	G	.	.	.	.	o.	.	.	o.—l.f.	o.
Betula alba	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bryonia dioica	.	.	o.	o.	.	r.	.	G	.	+	.	o.—l.f.	o.	.	.	o.	o.
Calluna vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Clematis vitalba	o.	.	.	.	o.	o.	o.	.	o.	o.	.	.	o.	o.	o.	o.	o.—l.f.
Cornus sanguinea	o.—l.a.	.	o.	+	o.	o.—f.	o.—l.f.	G	o.	.	.	o.	.	o.	f.	o.—l.f.	o.
Corylus avellana	.	.	.	.	.	.	.	.	o.	.	.	.	.	.	.	.	.
Crataegus monogyna	o.	o.	o.	f.	.	o.	o.	r.	o.—f.—l.a.	f.—a.	a.	a.—l.d.	a.—l.d.	a.	a.—d.	a.—l.d.	a.—l.d.
Euonymus europaeus	.	.	.	.	.	.	.	.	.	.	.	.	.	f.	.	.	.
Fagus silvatica	.	.	.	.	.	.	.	.	o.—l.d.	.	.	.	.	.	.	.	.
Fraxinus excelsior	.	one	.	.	r.	r.	o.	r.	o.	.	.	.	.	r.	o.	.	.
Hedera helix	l.	.	.	.	.	r.	.	.	.	.	.	.	+	o.	r.	.	o.
Humulus lupulus	.	.	.	.	.	.	.	.	.	.	.	.	l.	.	.	.	.
Ilex aquifolium	o.—f.	r.	.	.	o.—f.	o.	o.	o.	o.	.	.	.	.	f.	o.	m.	.
Juniperus communis	a.—d.	f.—a.	a.	o.—l.a.	f.	a.—l.c.d.	l.f.	G	r.	.	.	o.	.	o.	.	.	.
Ligustrum vulgare	r.—o.	.	.	.	o.—l.f.	.	.	.	.	.	.	.	.	a.	.	.	.
Lonicera periclymenum	o.	.	.	.	o.	o.	.	.	o.	.	.	.	.	o.	o.	.	.
Pinus silvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunus avium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. insititia	.	.	.	.	.	.	.	.	.	.	.	.	l.	.	.	l.	.
P. spinosa	o.	o.	o.—l.f.	o.	.	o.—f.—l.a.	o.	r.	l.f.	o.—l.f.	o.—f.	o.—f.	a.—l.d.	.	o.—l.f.	o.	f.—l.d.
Quercus robur	.	.	.	.	o.	.	.	.	o.	.	.	.	.	o.	one	.	.
Rhamnus catharticus	o.	l.	o.	+	o.	o.	l.f.	G	o.	.	o.	o.	o.	o.	f.—a.	f.	o.
Rosa arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r.	.	.
R. canina	.	r.	.	.	.	.	.	.	r.	.	.	.	.	.	r.	.	.
R. dumetorum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r.	.	.
R. micrantha	o.—f.	r.	.	.	o.	.	.	.	f.	.	.	.	.	f.	r.	.	.
R. rubiginosa	.	.	.	.	.	.	.	.	l.	.	.	.	.	.	.	.	.
R. sarmentacea	o.	.	.	.	o.	r.	.	.	o.	.	.	.	.	o.	o.	.	.
Rubus caesius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
R. fruticosus (agg.)	o.—l.f.	l.f.	o.	.	o.	o.	o.	G	o.—l.f.	o.	.	l.	.	d.	o.—f.	o.	o.
R. idaeus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ruscus aculeatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Salix caprea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sambucus nigra	l.	o.	o.—l.f.	f.—l.a.	.	o.	.	G	.	+	l.d.	o.—l.a.	a.—l.d.	l.	o.	o.—l.f.	o.—l.d.
Solanum dulcamara	.	.	.	.	.	.	.	.	.	.	.	.	.	o.	r.	.	.
Sorbus aria	o.	.	.	.	o.	o.—f.	f.—a.	o.	o.	.	.	l.	.	.	f.	+	o.
Tamus communis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r.	.	.
Taxus baccata	f.—a.	f.	f.	o.	d.	a.—d.	d.	d.	o.—l.d.	o.	f.	o.	f.—a.	a.	o.—f.	a.—d.	a.—l.d.
Ulex europaeus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viburnum lantana	.	.	.	.	.	.	.	.	o.	.	.	.	.	o.	.	.	.
V. opulus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

* The numbers indicate the number of clumps (maximum 4) fro

List of Species

8	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
				Hawthorn Sere (with ash)														Beech "system"								
	Developing yew-wood		Yew-wood	Scrub	Ash scrub		Yew-ash scrub								Yew-ashwood			Ash scrub		Ash-hazel coppice	Beechwood				Scrub	
gley ale	Hill-hampton Bottom (western slope)	Wascombe Bottom (western slope)	Kingley Vale	Downley Brow	Chilgrove Hill	Downley Brow	Kingley Vale (valley floor)	Chilgrove Hill clumps in grassland	Chilgrove Hill upper margin	Downley Brow lower margin	Downley Brow upper margin	Stead Combe upper margin	Holt Down	Stead Combe	Chilgrove Hill	Downley Brow	Kingley Vale	Chilgrove Hill	Downley Brow	Holt Down	Chilgrove Hill	Downley Brow	Holt Down	Stead Combe	Chilgrove Hill	Holt Down
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.	o.—l.a.	.	.	l.	l.f.	a.	o.—f.	o.	l.f.	o.	f.	o.	l.	o.	l.	l.	o.	1	o.	r.	.	.	.	G	.	.
l.a.	o.—l.f.	o.—l.f.	.	r.	o.	l.	o.	f.	f.	o.	f.	o.—l.f.	o.	o.	l.	l.	o.	3	o.	.	.	.	.	G	o.	.
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).	a.	a.—l.d.	.	a.—l.d.	f.	a.—d.	f.—d.	a.	f.	f.	a.—l.d.	a.	f.	f.—l.d.	l.f.	o.	o.	1	o.—l.d.	.	.	o.—l.f.	o.	r.	o.—f.	f.—l.a.
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ne	l.	.	r.	.	d.	f.—l.d.	o.—f.	f.	f.—a.	o.	f.—a.—l.d.	l.f.	a.—d.	a.—d.	a.—d.	o.	a.	4	a.—d.	o.—f.—l.d.	o.—l.d.	o.—l.d.	l.d.	o.	l.f.	.
).	o.	.	r.	.	o.	o.	o.	o.	o.	.	.	.	o.	o.	.	o.	.	.	r.	.	o.	.	.	.	.	.
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—l.f.	o.—f.	o.	.	.	.	.	o.	.	l.f.	.	.	one	.	.	l.	.	.	.	.	.	.	.	.	.	f.	.
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-	f.—l.d.	f.	.	l.a.—l.d.	.	o.	o.—f.	o.	o.—l.a.	o.	o.	o.—l.f.—l.a.	l.	l.	.	.	.	.	l.	.	.	.	o.	.	o.	.
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).	o.—l.f.	o.—l.f.	.	.	.	.	o.	o.	o.	.	o.	o.	o.	.	l.	.	+	1	.	.	.	l.	o.	.	l.	.
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.	l.f.	.	.	l.a.	o.	o.	f.—m.d.	f.—l.d.	l.f.—l.a.	o.	o.—l.a.	l.f.—l.a.	l.	o.	l.	.	.	3	o.	.	.	l.f.	l.f.	.	l.f.	.
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—l.f.	m.	o.	G	l.	f.—a.	o.—l.a.	o.—l.d.	.	o.—l.f.	l.	o.—l.f.	+	.	l.	.	o.	.	2	o.	o.	.	l.	l.d.	G	o.	l.f.—l.d.
.	o.	.	.	.	.	.	o.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	o.—l.f.	o.—l.f.	.	.	.	o.	.	+	o.	o.	o.	+	a.	o.	o.	o.	o.	1	o.—f.	o.	o.	o.	o.	.	o.—f.	o.
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.	a.—d.	a.—l.d.	d.	o.	o.—f.	o.—f.	f.—d.	f.	a.—d.	o.	f.—l.d.	o.—l.f.	a.—l.d.	f.—a.—l.d.	d.	d.	d.	2	f.—l.d.	f.	f.—a.	f.	a.—l.d.	o.—l.a.	f.	f.
.	.	.	.	.	.	.	o.—l.a.	.	l.	.	.	l.	.	.	.	.	.	.	.	.	.	.	.	.	l.f.	.
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which the species were recorded. + =present but frequency not recorded, but low. G=recorded from gaps. m.=marginal.

to yew-wood is rapid, whilst in the hawthorn sere it is much slower and may include intermediate stages with ash.

The size and height attained by adult yews decreases from the hawthorn sere with ash, through the hawthorn sere without ash to the juniper sere.

A comparison of the sizes of the yews in these valleys shows that the oldest yews grow in the most sheltered part and that size diminishes outwards. The juniper scrub may also form a centre from which the yews spread.

During development the yew kills out the scrub and forms a community, which, like the elephant herd, is socially well developed because of the longevity of the individuals. The vast majority of the yew seeds and seedlings are destroyed and when old yews die the re-establishment of a scrub protective of the few yew seedlings is prevented; the yew is unable to regenerate and the yew community dies out. This begins in the most sheltered part of the valley where colonisation first took place and spreads outwards leaving a gap where yew-wood once stood. A slow yew recolonisation of these abandoned areas is taking place.

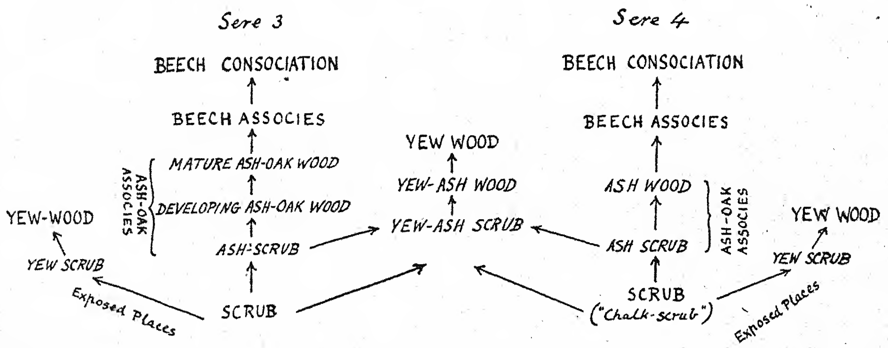
Ash, oak, and beech may grow in the intervals between the families of the developing yew society but because of the longevity of the yew and its capacity to endure shade, succession to yew-wood is not prevented, except sometimes perhaps by the beech.

As long as scrub maintains itself so long will the yew advance, and since hawthorn scrub is best developed to leeward yew advances most rapidly and abundantly eastwards, rather than westwards in the face of the prevailing winds.

Yew-wood is a single generation migratory community and owing to its dependence on scrub is best considered a society of scrub.

SECTION II. RELATION OF YEW-WOOD TO OTHER WOODY COMMUNITIES

The relationship between the two varieties of the hawthorn-yew sere and the normal succession of woody vegetation of seres 3 and 4[1] is presented schematically below.



[1] Watt. *L.c.* 1924.

In seeking to discover the relationship which the yew society bears to the normal succession, only the sere with ash need be considered since no direct evidence is obtained from a study of the variety without ash. By comparing seres 3 and 4 with the sere with ash it becomes apparent that the normal succession is arrested in the scrub or ash scrub stage by the spread of the yews, which by the formation of a closed society delay or check the invasion and development of ash-oakwood and beechwood. The relation of the yew to these later stages of the normal sere forms the subject matter of this section.

In the areas examined the full succession of each of the seres 3 and 4 is not seen, though stages representative of the general succession are found. No full treatment can therefore be given of the behaviour of the yew in the different seres of the South Down woodlands and while differences may be expected, they are probably not substantial as between the related seres 3 and 4.

The first requirement is a correct interpretation of the facts. For the woodland on Downley Brow an interpretation different from that of Adamson is given and my conclusion is supported from an analysis of similar woodlands on Chilgrove Hill and Holt Down. In these three areas I consider that we are dealing with two systems (designated briefly the *yew system* and the *beech system*) originating at some distance from each other on the same slope, with the beech system to windward of the yew system (see Figs. 4, 5, 6). To leeward of each the earlier seral stages are found. The generalised schemes of the two systems are as follows:

Yew system. Scrub, ash scrub, yew-ash scrub, yew-ashwood, yew-wood.

Beech system. Scrub, ash-oak associes (ash scrub, developing and mature ash-oakwood), beech associes, beech consociation.

The yew system was described in Section I. In no area examined is the full series of the beech system discovered but the evidence from the three woodlands mentioned previously is supplemented from Deep Combe and Stead Combe. Neither the scrub nor the beech consociation of the beech system has been observed in any of these areas.

The Beech System.

Ash scrub. Between the yew system and the beechwood on Chilgrove Hill (Fig. 6, 36) and also on Downley Brow (Fig. 5, 37) is a zone occupied by an ash scrub similar to that already described as the first stage in the development of the ash-oak associes from scrub[1]. It consists essentially of a hawthorn scrub freely colonised by ash with occasional trees of oak and beech, which on Downley Brow is also locally dominant. Most of the ash trees are young but a few are old. Old yews are occasional only (average girth of four trees on Downley Brow = 9 ft. 5 in.), and the yew families are largest and most

[1] Watt. *L.c.* 1924, p. 165.

frequent near to the yew system, becoming smaller and less frequent towards the beechwood. Hazel is a conspicuous shrub.

The origin of this ash scrub is clear. On Chilgrove Hill it consists of isolated, fused and fusing clumps of scrub with much young ash, separated in parts by enclaves of grassland. In the practically continuous and older ash scrub on Downley Brow the evidence is not so obvious, but in one gap were found *Gentiana amarella*, *Thymus serpyllum* and some grasses. These enclaves and relicts of grassland point to the superseding of grassland by scrub in which ash has become freely established.

On Downley Brow two gaps occur: one is due to the death of an old beech and bordered by two surviving and younger beeches, and now bears some *Sambucus* and *Rubus idaeus*; the other, formed by the death of two old beeches round whose stumps grows a scrub of *Rubus fruticosus* (agg.), *Cornus*, *Viburnum lantana*, *Clematis* and *Sambucus*, is now colonised by sapling ash.

In the Downley ash scrub there have been at least four beech clumps; two of these are noticed in the preceding paragraph; the third consists of a pioneer 20 ft. in girth at 3 ft. from the base, encircled by a number of semi-pioneers; the fourth is described in more detail. It is situated near the boundary between the yew system and the ash scrub and consists of six old beeches, five of which have the form of pioneers and one of a semi-pioneer. One pioneer is dead. Two survivors measured 15 ft. 4 in. and 16 ft. 4 in. in girth at 3 ft. from the base and are without doubt old trees. Under the beeches there are no shrubs, not even yews, but *Mercurialis* is occasional and small nibbled ash plants are frequent. The clump is closely surrounded by shrubs of which *Taxus* is dominant, but none of the encircling yews are large and all are clearly younger than the beeches.

Ash-hazel coppice. The ash-scrub in the two previous localities is replaced on Holt Down (Fig. 4, 38) by a coppice which is completely enclosed, on the north by yew scrub and yew-ash scrub and on the south by beechwood. Standards of comparatively young ash, beech and yew are found distributed in the coppice of hazel and ash: hazel (some probably planted) is dominant next to the yew-wood, and ash next to the beechwood. Here also grow *Sorbus*, *Sambucus*, *Euonymus* and *Clematis*, but with a low frequency.

Developing ash-oakwood. Flanking the beechwood in Deep Combe (Fig. 7) the ash-oak associes occurs—a narrow zone to the west, a wide zone of developing ash-oakwood (sere 3) to the east. Similar relations obtain in the adjoining valley of Malcombe, but here the ash-oak associes to the west is represented by a line of relicts on the beech associes of the plateau above. The developing ash-oakwood to the east of Malcombe belongs to sere 2. The structure, origin and development of these woods have already been described[1].

In the developing ash-oakwoods the yew has a varying frequency (occasional to frequent to locally dominant). All ages are represented from young yews

[1] Watt. *L.c.* 1924, pp. 160–176.

11 in. in girth to old yews 8 ft. 10 in. in girth. It is clear that regeneration is not prevented; but it is weak, and local dominance is due to older yews almost certainly established in the scrub or ash scrub which preceded the developing ash-oakwood. It is also significant that the yew is most frequent along the forward margin of the developing ash-oakwood (Deep Combe) where the wood is in a late ash-scrub stage. Immediately behind the yew society the yews are scattered except for one yew family. There is however no evidence to prove that the old yews represent the relicts of a once continuous yew-wood which has opened out with age and allowed the succession to ash-oakwood.

Mature ash-oakwood. Along the boundary between the yew-ash and beechwood at Stead Combe (Fig. 3) the ash-oak associes is represented by relicts; for the most part beechwood presses hard on the yew-ash scrub and yew-ashwood. Brief reference is here made to three of these relicts. Near the eastern end an enclave in the upper margin of the beechwood is dominated by *Fraxinus* and *Mercurialis* in their respective layers, the shrub layer being represented by occasional *Crataegus*: there is no *Taxus*. Midway along the slope there is an enclave dominated by *Quercus robur* and again there is no yew. But this associes is best represented in the south-west corner of the valley at the foot of the slope and adjoining the beechwood. The following are the chief woody plants and herbs:

Acer campestre	o.	Quercus robur	a.
Cornus sanguinea	o.	Taxus baccata (all comparatively young)	o.
Corylus avellana	o.	Dryopteris filix-mas	o.
Crataegus monogyna	o.	Fragaria vesca	f.
Fagus silvatica	o.	Mercurialis perennis	d.
Fraxinus excelsior	d.	Oxalis acetosella	f.
F. excelsior (young)	l.a.	Viola hirta	o.
Ilex aquifolium	o.	V. silvatica (agg.)	f.

The structure is that of a mature ash-oakwood. Yew is occasional, but despite the proximity of old yews there are no old plants here.

Beech associes. Beechwoods in the associes stage are found on the windward side of the woodland strips on Chilgrove Hill (Fig. 6, 39), Downley Brow (Fig. 5, 40) and Holt Down (Fig. 4, 41); on the lower part of the southern slope of Stead Combe (Fig. 3, 42); and in the valley bottoms and neighbourhood of Deep Combe and Malcombe (Fig. 7). The beechwoods in the first three localities are little more than very large clumps.

The structure varies considerably in the different localities, and with the dominant beeches there grow ash and oak varying in amount according as the associes is in an early or a late stage. On the exposed slopes enclaves may be filled with a scrub colonised by secondary and dependent ash[1], which on Holt Down is coppiced. The shrubs and ground flora vary with the canopy.

All forms of the beech, from aged pioneers to young erect stems, are represented; young stems predominate in the developing associes, but on Holt Down most of the trees are old. The "parents" of the Stead Combe

[1] **Watt.** *L.c.* 1924, p. 160.

wood are probably five very old dead and dying pioneer beeches found along the slope about the middle of the wood; and of the Downley Brow wood two old pioneers (17 ft. 3 in. and 12 ft. 10 in. in girth at 24 to 30 in. from the base) growing near the southern margin. Pioneer oak and ash are also occasionally found.

In all cases the direction of spread is mainly towards the yew system. This is confirmed from the occasional beech invaders in the ash scrub of Chilgrove Hill and Downley Brow, and in the ash-hazel coppice of Holt Down; and from the included ash and oak along the boundary between the beechwood and the yew-system of Stead Combe.

North-east of Malcombe yews are occasional to locally frequent in the young beech associes; elsewhere in the late beech associes in the neighbourhood of Deep Combe and Malcombe they are sporadic or even absent, despite the proximity of fruiting yews. Frequently those that are found grow near and under the immediate canopy of ash or where the beech canopy is more open. In the beech associes of the other areas yews are frequent.

The yew trees vary much in form and condition. Occasionally old pioneers are found, as for example locally in the forward margin of the beech associes in Stead Combe, where the old yews have been included, and near the southern edge of the Downley beechwood, where two pioneers grow measuring 9 ft. 1 in. and 9 ft. 5 in. in girth; but the majority of the trees are young and have obviously grown up under the beech canopy. These young trees are for the most part spire pointed, diffusely branched with scanty foliage—the leaves persisting on the secondary branches about 4 years only, and although surviving longer on the main branches are scattered. Under richly branched beeches occasional yews are flat topped, while under pioneer beeches no young yews grow. The young yews are obviously unhappy and whether they set seed is doubtful.

One instructive old dead yew was found in the late beech associes above Malcombe. It was about 2 ft. in diameter and of pioneer form but it had produced from near the base an erect stem which had grown to a height of about 30 ft. and a basal diameter of 8 in. This stem, an obvious accommodation to new canopy conditions, had also died.

Scrub. To windward of the beech associes on the slopes there grows a scrub which varies in composition but shows similar structure. It consists of isolated bushes and scrub clumps in which trees may or may not be established; yew is an invader in all areas. The Holt Down scrub is shown in Pl. V, Phot. 6. The beech associes is either not invading this scrub at all, as for example on Holt Down, or is pushing into it very slowly as on Chilgrove Hill and Downley Brow. These areas demonstrate the quick transition from scrub to beechwood of exposed slopes[1].

[1] Watt. *L.c.* 1924, p. 182.

THE RELATION OF YEW TO WOODS OF ASH-OAK AND BEECH.

The status of the yew communities has already been determined; it is a society of scrub. This does not exclude it from occupying a position in ash-oakwoods or beechwoods, but in this case the yew society is in them but not of them. For the case is quite conceivable, although a yew society in beechwood has not come under my observation, that the migrating yew society may be overtaken and surrounded by oncoming ash-oakwood and beechwood, and yet owe nothing to them for its establishment or maintenance.

In the woodlands examined we have seen that the yew society may originate in scrub or in ash scrub, but no example of establishment in developing ash-oakwood, mature ash-oakwood, beech associes or beech consociation has been observed. The later stages of the normal sere do not seem to favour yew society establishment. The relation of the yew to different kinds of woody communities will now be discussed.

Relation to scrub. This has been discussed; the yew society may develop here.

Relation to ash scrub. The evidence from Chilgrove Hill and Downley Brow shows that the yew society may also develop here.

Relation to developing ash-oakwood. In the developing ash-oakwood there is a breaking down of the typical scrub structure and a building up of the typical forest structure. Both in Deep Combe and in the adjoining Malcombe yews grow in this stage. Some are obviously included from scrub but some have grown up under the new conditions. These however show no definite movement towards the formation of a continuous canopy and the development of a true society. Yew may be a locally abundant constituent but local dominance is excluded, apart of course from the local dominance of a group of yews surviving from scrub or developed in ash scrub.

Relation to mature ash-oakwood. In the small areas of mature ash-oakwood in Stead Combe, yew is only an occasional constituent despite the proximity of abundant and old yews. In other woods previously described[1] yew may however be much more conspicuous; and is on the whole more frequent in sere 3 than in sere 2.

Relation to beechwood (beech associes and beech consociation). On p. 191 of the work cited the statement is made that as development of the beech associes proceeds the yew is gradually eliminated; and this is true of the beechwoods in the neighbourhood of Deep Combe and Malcombe. In the beech associes of Chilgrove Hill, Downley Brow, Holt Down and Stead Combe the frequency of the yew varies but is on the whole high. In the beech consociations of the plateau yew is infrequent and Adamson states that "in the majority of existing beechwoods *Taxus* is only an occasional tree[2]." In the "beechwoods on chalk" (sere 4) he further says, "The yew is present in

[1] Watt. *L.c.* 1924, pp. 165–171. [2] Adamson. *L.c.* 1922, p. 209.

all of them, but is not abundant except in Head Down Hanger; in this wood the yew is locally subdominant and in the degenerate wood at Downley Bottom it becomes locally dominant[1]." Regarding Head Down Hanger the following is a transcript from my notes made during a brief visit: "Much *Taxus*, mostly young. Middle aged yew dead under pure beech canopy but young yews surviving with few or short lived leaves."

The general condition of the yews varies with the density of the canopy. Between the normal healthy yews growing under an open canopy and the poorly developed flat-crowned yews under beeches of semi-pioneer form there are all transitions. Under richly branched and heavily foliaged beeches the yew is absent.

The shade-bearing capacity of the yew, the greatest among native trees, is pointed out by most writers, but according to Jaennicke[2] the tree is sensitive to long continuing shade; and according to my own observations the yew does not grow well under a *continuous and closed* canopy of pure beech. Exactly how long it survives is not known, but the majority of the yews observed are young. On yews growing under these conditions ripe fruits have not been seen.

Perhaps too much stress is laid upon shade as a factor limiting the growth of plants under woodland canopy. Root competition is an important and sometimes a deciding factor, but the yew shares with the beech the capacity to grow on shallow calcareous soils and its root system is probably as efficient as that of the beech.

The yew has a low specific conductivity (12 ± 2)[3], but unlike *Ruscus aculeatus*, *Daphne laureola* and many conifers it can grow in dry places subject to drought: it is a soil xerophyte but not a dry climate plant. Conwentz[4] reports that in the district of Heidenau, Bavaria, "shade" yews, when exposed by the removal of the spruce and beech canopy, were observed to sicken and die.

In the woodlands described here the yew attains larger dimensions in the hawthorn sere of deeper soils.

The example described of a yew which exchanged its pioneer form for the diffuse shade form to suit the new conditions is paralleled among scrub elements, for example by *Crataegus*, which is a bushy plant in the open but assumes the shade form under canopy. The death of "open" forms under shade and their replacement by shade forms either from the same stock or by new individuals is a subject requiring fuller investigation than has hitherto been accorded it.

A thicket scrub of hawthorn may be impregnable to trees, but under canopy there is no hint of *Crataegus* forming a definite closed society. *Taxus* seems to behave in a somewhat similar way, forming a society in the open,

[1] **Adamson.** *L.c.* 1922, p. 121.
[2] **Jaennicke,** quoted by **Kirchner, Löew** and **Schröter.** *L.c.* 1908, p. 62.
[3] **Farmer,** *Proc. Roy. Soc.* Ser. B, **90,** 1919, p. 218.
[4] **Conwentz.** *Engl. Bot. Jahrb.* Beiblatt **46,** 1912, p. 48.

but although sometimes locally abundant in woods of ash, oak and beech it seems unable to form a closed canopy under such conditions.

Yew regeneration is of course severely handicapped by animals which destroy the seeds and eat the seedlings and older plants. And this factor is undoubtedly important, though it is not offered as a full explanation of the inability of the yew to form a closed canopy in ash-oakwoods and beechwoods.

The Interpretation of Chilgrove Hill, Downley Brow, Holt Down, Stead Combe and Deep Combe Woodlands.

Yew system. The development of the yew system has been discussed in Section I.

Beech system. On Chilgrove Hill, Downley Brow and Holt Down only two stages of the complete normal sere of woody communities are found, viz. ash scrub (and coppice) and the beech associes. The ash scrub of Chilgrove Hill still shows the clump structure and enclaves of grassland, that of Downley Brow is in a later stage of development but relicts of grassland occur.

The beechwoods of these slopes resemble the beech associes of exposed slopes in which ash and oak are secondary and dependent, filling up the intervals between the beeches. On the windward side the ash-oak associes is not developed on Chilgrove Hill and Holt Down but is represented by patches of ash scrub on the more sheltered southern end of Downley Brow. In all, invasion of the ash scrub and coppice to leeward is taking place.

The relation of the ash scrub to the beech associes is clear; the ash scrub is the early stage of the ash-oak associes developed to leeward of beechwood and compares in structure with ash scrub as described in previous work.

To leeward of the beechwood in Deep Combe the normal succession is found—scrub, ash scrub, developing ash-oakwood—but as yet sufficient time has not elapsed to allow the ash-oakwood to attain to maturity of structure. Locally the developing ash-oakwood is hemmed in between the yew society, which occupies the position of the ash scrub, and the beech associes advancing from the valley: in part the beech associes abuts directly on the yew society.

A later stage in this process of obliteration is demonstrated in Stead Combe, where for the most part the beech associes, probably derived from a few pioneers still extant, presses hard on the yew system. There is clear evidence to show that an ash-oak associes has been overcome by the beech associes advancing toward the yew-wood; relicts of mature ash-oakwood are found.

From these areas an almost complete normal sere of woody vegetation can be reconstructed. This is in conformity with the development of the woody vegetation described in previous work.

THE ORIGIN OF THE YEW-WOODS AND THE PLACE OF YEW IN THE BEECH SYSTEM.

In only one of these five areas—Deep Combe—is there evidence to show that the yew society has migrated from its original position. Subsequent to its withdrawal the woody communities of the normal sere have originated in, and progressed outwards from, the valley.

In Stead Combe it has been shown that the oldest yews grow on the slope near the south-west corner of the valley. There is no evidence that yew-wood ever existed on the site now occupied by beechwood, and if scattered pioneer yews ever grew there they have quite disappeared. Difficulties in the way of yew establishment and extension were pointed out in the study of the woody vegetation on the floor of Kingley Vale, and the observations from Downley Brow and Chilgrove Hill emphasise these obstacles on the gentler lower parts of these slopes. To detail the exact course of the development of woody vegetation on the lower slopes of Stead Combe is impossible, but the evidence justifies the conclusion that a succession of hawthorn scrub, ash-oakwood and beechwood has taken place.

On the three slopes, Chilgrove Hill, Downley Brow and Holt Down, there is again no evidence to show that the yew-woods have withdrawn from their original position or are migrating as a whole along the slope. This simply means that the yew society is comparatively recently established and that the original colonists are still extant: that the yew society will migrate, under conditions similar to those existing, seems clear. That migration and subsequent colonisation by ash scrub and beechwood has taken place is negatived by the occurrence of scattered old pioneers in the beech system. These pioneers are old, but none are quite as large as the largest yews measured in the latest stage of development represented in the adjoining yew system; they are however of the same order of magnitude.

From internal evidence the early history of these woodlands can be reconstructed. In a hawthorn scrub scattered in the grassland of the slopes, appeared yew invaders. The scrub to leeward, benefiting from the shelter of that on the windward side, developed more quickly and allowed a more rapid growth of the yew families in the position now occupied by the largest yews. The increased shelter thus afforded by the wind-resistant yew promoted the spread of scrub to leeward and with it the extension of the yew, the growth of yew families and the differentiation of the seral communities.

The development of the vegetation windward of the yew system can best be explained by picturing the state of the vegetation before the establishment of the beech and the beech associes: this is materialised in the scrub south of the beech associes on Holt Down, which consists of a scattered hawthorn scrub with scrub clumps and yew invaders (Pl. V, Phot. 6). Since the position of this scrub was to windward, development both of the scrub itself and of the

yew families was very slow and quite old yews occurred scattered in the open scrub. The establishment of the beech and its subsequent development to woodland provided shelter and stimulated the growth of scrub, which rapidly filled up the intervals between the original clumps and permitted the growth and spread of ash, hitherto absent or rare in the exposed open scrub. The spread of the scrub allowed more rapid increase in the size of the yew families.

This hypothesis conforms to the known behaviour of ash, beech and yew and explains the distribution of old pioneer yews both in the ash scrub and in the beech associes. The frequency of hazel in the ash-hazel coppice is in conformity with its frequency in the ash scrub of the beech system.

On Downley Brow, in addition to the young beech invaders, there are four clumps. In these all the trees now living are old, of pioneer and semi-pioneer form, and have grown up in open conditions such as prevailed during the early stages of vegetational development windward of the yew system. In the open scrub with yews of that period, pioneer beeches had become established. Three of them at any rate have reproduced and formed a family, but no further extension has taken place. These clumps are degenerating, but they are not considered to be the remnants of an original beechwood but pioneer clumps which have failed to extend.

Of the woods considered by Adamson to be degenerate[1], two are included in the present account, viz. Oxenbourne Down (eastern slope of Wascombe Bottom) and Downley Brow. The Downley yew-wood he considers as having arisen from a beechwood from which the dominant trees have been removed or died and he finds in the degenerate beech clumps and in the presence of some woodland plants such as *Arum maculatum* and *Mercurialis perennis* evidence of previous continuous woodland cover. He also sees in the present distribution of the beech clumps the progression of destruction of the beech forest. The origin of the Oxenbourne wood is not so obvious, but he classes it along with the Kingley Vale yew-wood and considers both as a subclimax due to the destructive action of rabbits in large numbers.

The following criticisms of this view are offered:

1. The presence of *Mercurialis perennis* and *Arum maculatum* cannot be held as reliable evidence for the former existence of woodland because both occur in places reproducing woodland conditions, e.g. under scrub and by hedgerows.

2. On Downley Brow the beech clumps consist of trees showing pioneer or semi-pioneer forms which could only have appeared in open conditions. Further there is no relation between the supposed progression of beechwood destruction and the stage of development reached by the yew-wood.

3. The view does not explain the occurrence of old pioneer yews in the beech system: yews grown under canopy do not develop bush or pioneer forms.

[1] **Adamson.** *L.c.* 1922, pp. 206, 208–210.

4. The phenomena of invasion and succession are left unexplained.

5. On *a priori* grounds it seems possible that yew-woods could arise from beechwoods, but there is no good evidence to support this view: in fact, the evidence from the plateau woods shows that the yew tends to disappear from the later stages of the beech associes.

STATUS OF THE ADULT YEW COMMUNITY.

The preceding analysis shows that the yew loses its high sociability value in the woodlands leading to the beech consociation; in these, in fact, the yew community disintegrates.

The determination of the status of the adult yew community in the vegetation of the South Downs is based on the well-attested belief that the beechwoods are progressive. On the calcareous soils of areas not yet or but insignificantly invaded by the beech—the Downs east of the Arun, Butser Hill and much of the lower dip slopes of the western wooded area—grassland predominates, and scrub with yew societies is found in valleys and sheltered places. This is believed to represent the original condition of the vegetation in areas now wooded. Grassland is climax and the yew forms a society in post-climax scrub, growing in areas whose local climatic conditions favour the development of woody communities. On slopes similar favouring conditions are provided by the coalescent yew groups to leeward of which invariably occurs the main development.

On these calcareous soils formerly dominated by grassland the arrival of the wind-resistant beech provides the conditions necessary for the extension of scrub and woodlands of ash and oak. Although yews are found in this scrub of the main line of succession, there is apparently no time for the development of the yew society which is not normally found there. Occurrence within the main line, as at Deep Combe, is due to a society of the original scrub being overtaken in its migration by the faster moving ash-oakwoods and beechwoods, in which the yew society disintegrates. The yew society is therefore not a normal constituent of the succession leading to beechwood and in Clement's nomenclature is a relict society.

In summary we may say that the adult yew community is a society of the original post-climax scrub and a relict society in the succession culminating in the present progressive beechwoods.

SUMMARY OF SECTION II.

The analysis of five South Down woodlands shows that one part consists of a series of stages leading to pure yew-wood, the other to beechwood. These are called respectively the yew system and the beech system. In no one area are all the stages of the beech system found. The following is the generalised succession:

Yew system. Scrub, yew-ash scrub, yew-ashwood, yew-wood.

Beech system. Scrub, ash-oak associes, beech associes, beech consociation.

In four woodlands the yew system extends to leeward of the beech system; the fifth grows on a sheltered valley slope.

The structure and development of the yew system is described in Section I. It is believed that the yew-wood originates by yew invasion of a scattered scrub growing on a slope. Development and differentiation of the seral stages take place to leeward, whilst to windward the scrub remains in an open condition.

The beech system is believed to arise subsequent to the establishment of a protective woodland of wind-resistant beech. To leeward succession proceeds through scrub to ash scrub, developing and mature ash-oakwood, beechwood. The ash-oak associes may be artificially stabilised as coppice.

The relation of the yew to these woody communities is discussed. The yew society may arise in scrub and in ash scrub, but although yews may be locally abundant in developing and mature ash-oakwood and in beechwoods, there is no good evidence to show that a yew society can be formed there. The inability of the yew to grow well under a continuous and closed canopy of beech is pointed out.

Previous views on the origin of yew-woods are criticised chiefly on the ground that they fail to explain the phenomena of development described in this paper.

The fact that all the yew-woods described both in Sections I and II are remote from or on the outskirts of blocks of progressive woodlands of ash-oak and beech is evidence in favour of the interpretation put forward.

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THE VEGETATION AND RETROGRESSIVE CHANGES OF PEAT AREAS ("MUSKEGS") IN CENTRAL ALBERTA

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(*With Plates VI–X, Folding Map, and six Figures in the Text.*)

CONTENTS.

INTRODUCTION

In the present paper the plant communities and certain retrogressive changes on small well-defined peat areas in the Edmonton district will be described, and the origin of the peat deposits discussed.

In Canada the term "muskeg" is applied to areas of peat covered with a certain type of vegetation. The term is practically synonymous with peat-bog. *Sphagnum* is usually a much more pronounced feature in the peat areas of Canada than it is in northern England and Scotland, and trees of small or moderate size frequently occur on these areas. These features often give a very different impression to the usually treeless areas of Northern Britain. Many plants are common over these areas in both countries, but in Canada *Ledum groenlandicum* takes the place of *Calluna vulgaris* as the dominant shrubby ericaceous plant. It will be convenient in considering the distribution and succession of the vegetation if a brief description of the topography and meteorology of the district is given first.

TOPOGRAPHY

All the peat areas to be described lie within 30 miles of Edmonton, on the last step of the plateau east of the Rocky Mountains, which rise about 200 miles due west of Edmonton. The general altitude varies between 2180 ft. (Edmonton) and 2500 ft., the country being gently undulating except along the main river valleys, which usually descend abruptly to 200 ft. below the plateau, with steeply sloping gorges where tributaries enter the main valley.

Reference to the map will show, to the east and south-east of Edmonton, areas in which lakes occur in great abundance, varying in size from Cooking Lake, 9 miles long and from $\frac{1}{8}$ to $4\frac{1}{2}$ miles wide, to small pools 300 ft. across. Over an area of 400 square miles there are several hundred lakes large enough to be marked on a scale of 3 miles to 1 inch, and the total number, including the smaller lakelets, is probably greatly in excess of this number.

Much of the lake country differs somewhat in topographical features from that found elsewhere. Little hillocks abound, seldom more than 15 or 30 ft. high, often connected by curving ridges with flat basins between, and it is in these basins of varying size that the lakes and muskegs occur. All this country lies within the 2400 ft. contour line and therefore forms a plateau about 300 ft. above the country eastward which drains immediately into the Saskatchewan Valley. None of the lakes is of any depth, the maximum in Cooking Lake being 18 ft. whilst most of them are from 6 to 12 ft., and may be described as flat-bottomed basins lying on drift. The general flora of the waters is prolific, members of the Cyanophyceae being abundant, with many diatoms, a general absence of desmids, and a scarcity of filamentous members of the Chlorophyceae (see List, pp. 331–2). The lakes are frequently bordered by a zone of Carices and Scirpi, backed by zones of willow or spruce.

METEOROLOGY

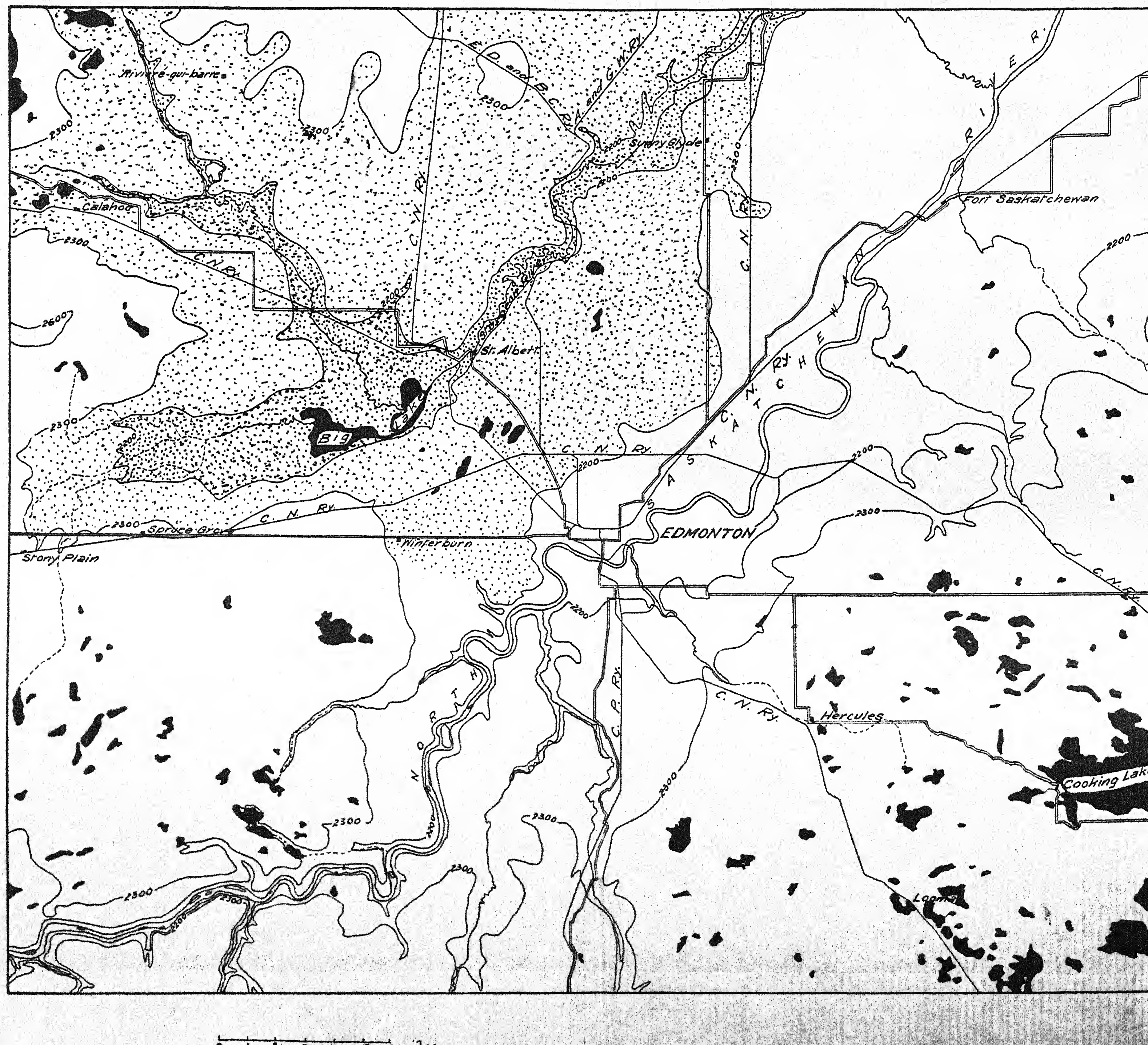
Very few data exist except figures for rainfall and temperature, and even these records are available only for a few stations, are often imperfect, and do not extend over many years.

The rainfall records for three widely separated stations, North Cooking Lake about the centre of the lake area, Rocky Mountain House, 90 miles south-west of Edmonton and 60 miles from the mountains, and Red Deer, 100 miles south of Edmonton, are given below.

Annual Precipitation (inches).

	1916	1917	1918	1919	1920	1921	1922	1923	1924
Athabasca	—	—	—	*	22·87	14·69	13·44	14·95	18·34
North Cooking Lake	—	—	14·58†	15·33	19·53	14·00	12·85	16·99	18·27
Red Deer	22·79	16·58	*	13·40	12·81	*	12·21	22·92	20·07
Rocky Mt. House	—	22·53†	18·95‡	*	*	—	9·56§	*	18·14

* Incomplete returns. † Jan.–Feb. missing. ‡ Oct. missing. § July–Aug. missing.



Sketch-map of the country round Edmonton, showing the lake country in the south-east, where at Cooking Lake and Looma, muskegs described in this paper are situated; and the Sturgeon River basin in the north-west (stippled dark below 2,200 feet, light between 2,200 and 2,300 feet), at the upper end (south-west corner) of which the Stony Plain muskeg and lake, also described, are situated.

The earliest records do not date back farther than 1916, and some years are so incomplete that they have not been included; in others which are less so, the months that are missing have been indicated.

It is impossible to draw any certain conclusions from these records except that the rainfall is about 15 in. per year in the lake region, at Rocky Mountain House about 18 in. and at Red Deer about 16 in. Much of this comes as snow during the winter months but varies from 6 in. or even less in some years to a total winter fall of 5 or 6 ft. in other years. We are indebted to Sir Frederick Stupart, Director of the Dominion Meteorological Service for these figures. The difficulty of maintaining continuous records in sparsely settled districts must be great, and this was much accentuated during the later years of the war. The need of more scientific study of meteorological conditions such as light intensities, evaporation, relative humidity and wind movements, is obvious, the more so as climatic conditions are more variable in the north-west of Canada than anywhere on the Continent.

Probably no year ever occurs when the muskegs are not frozen continuously between early October and the latter part of April. Activity of the vegetation is thus limited to five months of the year or even less. Owing to high temperatures and frequent unclouded skies during the growing season, temperature gradients in peat areas are extremely abrupt. Thus in June or July with a shade temperature of 90° F. at the surface of the muskeg, the ground may be frozen 18 in. below the surface, and in many of the muskegs in which there is little or no circulation of water, the layers 2 ft. below the surface remain permanently frozen. Since many of the muskegs are not more than 100 yds. in diameter and are surrounded by banks of dark alluvial soil covered with poplar and grassland and sometimes cultivated, no greater contrast of conditions or vegetation within a small distance could well be found.

During the winter, humidity is nearly always extremely low and although it may attain a high value for short periods in the summer, the mean value is usually small. As regards rainfall, humidity and temperature, the climatic factors are not those usually associated with rapid or extensive peat formation, and the retrogressive changes seen in so many of the muskegs would probably be more marked were they not frozen for about seven months in each year.

VEGETATION OF AREAS NOT COVERED WITH PEAT

The area under discussion lies near the northern boundary of the parkland that stretches across the central region of Alberta and is bounded on the north by coniferous forest and on the south by northern prairie, which differs essentially in climatic features and vegetation from the semi-arid prairie lying farther south. The parkland belt in the meridian of Edmonton is about 160 miles in width and extends 40 miles north of the Saskatchewan River. It may be regarded as a transition zone between the prairie and the northern coniferous forest. Originally this undulating plateau was fairly continuously

covered by various species of poplar and shrub thickets. The dominant tree is *Populus tremuloides* Michx. and although much has been cleared for agricultural land, probably the major part of the area is still tree-clad. Accompanying the dominant species of poplar are several others, *P. deltoides* March, *P. sargentii* Dode. and *P. balsamifera* L. being locally abundant. Thickets of *Salix* are frequent, and throughout the country may be found *Picea albertiana* G. Brown (the western form of *P. canadensis*) occurring either singly or in groups and frequently becoming the chief tree in the river valleys and ravines. The coniferous covering is greatly extended by the numerous muskegs in certain regions. The chief tree here is *Picea mariana* (Mill) B.S.P. (black spruce), although *Larix laricina* (Du Roi) Koch frequently accompanies it. Birch is not abundant and chiefly occurs on the sides of some of the valleys and on muskegs.

The flora of the poplar woodland consists of a number of shrubs, among which species of *Rhamnus*, *Lonicera*, *Ribes*, *Rosa*, *Alnus*, *Salix*, *Shepherdia*, *Eleagnus*, *Prunus*, *Amelanchier*, *Symphoricarpus* are most noticeable, while the ground flora includes *Linnaea*, *Disporum*, *Mertensia*, *Potentilla*, *Mitella*, *Pyrola*.

The contrast of this form of vegetation, so uniform over large areas, with the plants found on the muskegs is very great, and is accentuated by the small size of many of the muskegs and the very narrow transition zone—often only a few feet across—from one type to another.

DISTRIBUTION OF MUSKEGS

While the two areas mentioned have been selected for description it may be of interest to indicate briefly the main features of muskeg distribution over larger contiguous areas. Muskegs at various stages of development or retrogression are of course confined to the parkland and coniferous forest to the north and are quite unknown in the prairie regions. In the parkland there is a progressive increase to the north and to the west. The most southerly muskegs observed are in the region of Lacombe, 87 miles south of Edmonton, and thus approximately 33 miles north of the southern boundary of parkland, but farther west examples occur in a more southerly position. A marked feature is their constant association with regions of lakes.

The distribution of peat areas is not indicated on any topographical or geological maps, and for this reason any account of their distribution in such a wide stretch of country must necessarily be imperfect. Generally speaking, the areas increase in extent west and north-west of Edmonton and on approach to the coniferous forest, continuous areas many miles in extent are encountered. Some of these larger areas have a different vegetation and probably vary in their developmental history from the small basins in the Edmonton district, but nothing has yet been recorded regarding these features, and from a botanical point of view they are quite unknown. Peat-covered areas are

unknown in the Eastern Rocky Mountains, but in the foot-hill region north of the Edmonton parallel they frequently cover large stretches of country. Their association with moraine remains can be noted in all districts.

VEGETATION OF THE MUSKEGS

(*a*) Cooking Lake District.

Between Edmonton and the northern shore of Cooking Lake lies a succession of muskegs occupying small, shallow and sharply defined basins. A number of these have been examined and two representative types are described here. Owing to the scarcity of place names on the maps, all the muskegs are designated by serial numbers and are so referred to in this paper.

No. 1 occurs 9 miles south-east of Edmonton and its topography and general features are shown in Fig. 1 and illustrated in Pl. VI, Phot. 1.

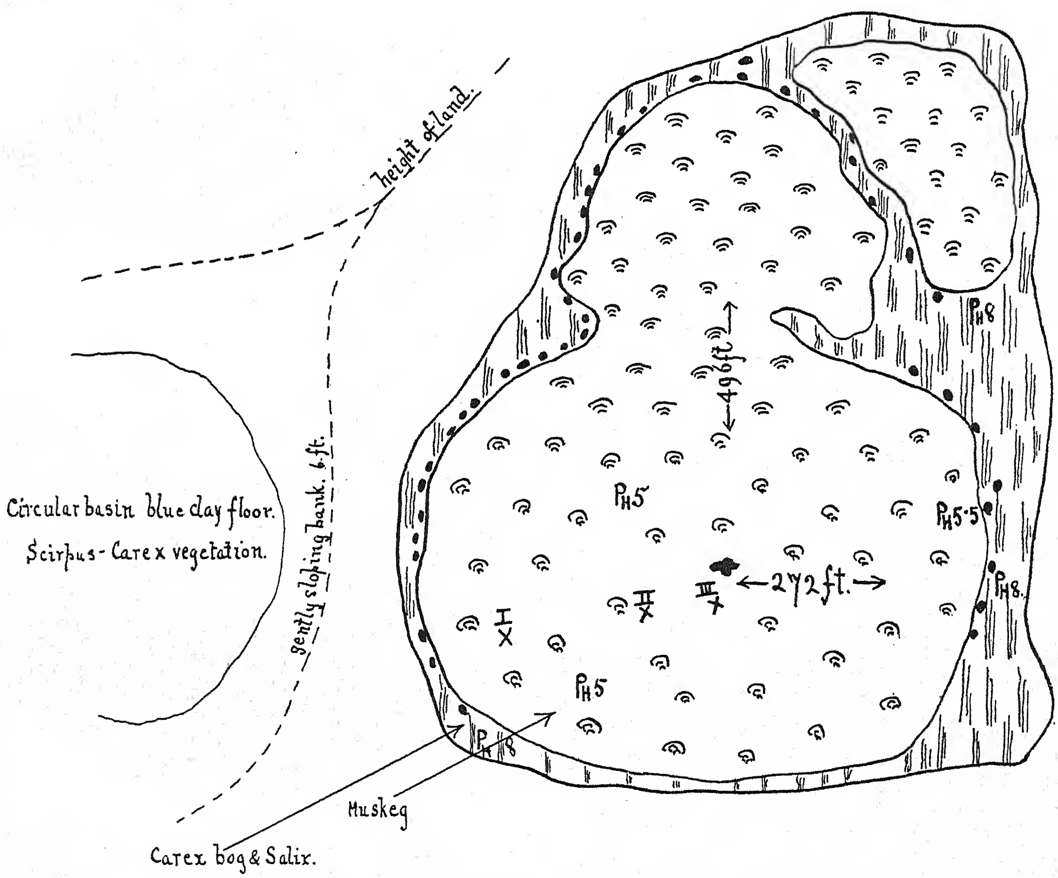


FIG. 1. Muskeg No. 1 in shallow clay basin surrounded by morainic banks.
P_H = Hydrogen ion concentration. For Vegetation, see Plate VI, Phot. 1.

The vegetation tends to be uniform and the dominant species are: *Ledum groenlandicum* Oedr., *Sphagnum acutifolium* var. *rubellum* (Wils.) Russow., *Vaccinium vitis idaea* L., *V. oxycoccus* L., *Rubus chamaemorus* L.

Subordinate species are: *Vaccinium canadense* Kalm., *Eriophorum vaginatum* Torr., *Vagnera trifoliata*, *Cladonia pyxidata* Hoffm., *C. rangiferina* Web., *Peltigera* sp., *Polytrichum commune* L., *P. juniperinum* Willd.

The growing centre of the muskeg consists of a small irregular extent of water a few feet across bordered by *Sphagnum* on which grow *Vagnera trifoliata*, *Vaccinium oxycoccus*, *Eriophorum vaginatum*, and *Larix laricina*. A few small patches of *Menyanthes trifoliata* occur in the pool, this being the only spot on the muskeg where this plant is found. This ecological centre is surrounded by mounds of *Sphagnum* somewhat drier in character, bearing *Ledum groenlandicum*, *Polytrichum commune*, larch and seedling birch.

The whole muskeg is dominated by actively growing *Sphagnum*, wet and spongy, forming mounds about 8 to 12 in. above the intervening hollows. Very little zonation of vegetation is to be seen, but as the outer zones of the muskeg are approached *Vaccinium vitis idaea* becomes relatively more abundant and *Vaccinium oxycoccus* decreases in amount. It will be seen from the sketch-map that the muskeg lies in a small basin and is surrounded by a border of *Carex* bog varying slightly in width, with a zone of Salices and *Alnus* close to the muskeg. The arrangement is symmetrical and the transition from the *Carex* bog to the sloping banks with *Populus tremuloides* and the usual ground flora is most abrupt. Borings were taken at several points marked on Fig. 1. The general depth of the basin is 8 ft. below the present surface of the muskeg, and the underlying material found in the borings is a stiff blue clay containing numerous grains of rounded quartz. This clay is described more particularly for Stony Plain muskeg. The peat immediately overlying the clay is not formed of *Sphagnum* and seeds and fruits of *Potamogeton* sp., *Menyanthes trifoliata* L., *Potentilla comarum* L. and *Carex* sp. have been collected from it. Thus the vegetation in this small basin was that of a shallow lake which in the course of time gave place to a peat bog vegetation.

Most of these muskegs are clad, to a varying extent, by fairly large trees of black spruce, birch and larch. This condition seems to have persisted for a long time as tree remains are found in this muskeg, as far as can be ascertained by borings, throughout the peat layer. Although the trees are relatively small, many are of considerable age and certain features connected with their rate of growth will be described in this paper. The present surface water has a pH 5 over the whole muskeg, but on the *Carex* bog only a few feet away from the margin of the muskeg values of pH 8 are obtained.

The topography in which this, and all other muskegs in this area occur calls for brief description. Everywhere are mounds and curved ridges enclosing small basins. The mounds and ridges are of slight altitude, usually about 10 to 30 ft. high and resemble well preserved morainic ridges and mounds.

Phot. 1. Cooking Lake, No. 1 Muskeg (pp. 321–2).

Phot. 2. Circular basin with floor of blue clay and *Carex* bog.

Phot. 3. Margin of Cooking Lake Muskeg No. 2. Raised muskeg to left and abrupt descent to surrounding *Carex* bog (p. 322).

The material of which the ridges are formed, however, is a yellow clay in which occur scattered boulders of great size. The clay underlying the muskegs in the basins is dark blue-grey with rounded quartz grains, from mere specks to about 5 mm. in diameter. The system of mounds and ridges and the material of which they consist, suggests deposition by water action at the retreat of the ice-sheet.

No. 2 muskeg occurs about half a mile east of No. 1. Its area is about the same, but important retrogressive changes have taken place. The whole muskeg is closely covered by *Ledum groenlandicum* with *Sphagnum*. The flora is essentially similar to that of No. 1 but the relative abundance differs, inasmuch as *Sphagnum* shows disintegration, particularly on the southward side of the mounds. Seedling trees do not occur in such abundance, and plants associated with the active growth of *Sphagnum*, such as *Vaccinium oxycoccus*, are not so frequent. The salient feature consists in the distribution of vegetation types in the small basin in which the muskeg is situated. The muskeg is surrounded by a zone varying from 20 ft. to 100 ft. of *Scirpus* bog and exists as a platform raised about 3 ft. above the encircling *Scirpus* zone. The border in some places is abrupt and the banks steep, but on the south margin, where the *Scirpus* zone is broadest, the muskeg is scattered and occurs as isolated patches separated by channels of *Scirpus*. The flora of the isolated muskeg mounds consists of *Eriophorum vaginatum*, *Scirpus caespitosus* with *Ledum groenlandicum*, *Polytrichum commune* and a slight amount of *Sphagnum*.

The broad zone of *Scirpus-Carex* bog, the raised platform of muskeg within, the scarcity of *Sphagnum* and the dominance of *Ledum* over the whole peat area, are the chief features of interest in this area.

(b) LOOMA DISTRICT.

This region is intersected in all directions by a network of small shallow lakes containing luxuriant vegetation which appears to consist mainly of *Utricularia intermedia* Hayne, *Potamogeton* spp. and an algal flora of which members of the Cyanophyceae—particularly *Nostoc*—are the chief constituents. It is difficult to examine the flora of most of these lakes as they cannot be approached during the summer owing to their being surrounded by a margin some hundreds of feet wide of liquid peaty clay more than 10 ft. in depth. Shallow basins of smaller size and tending to be circular in outline are occupied by muskegs. The whole topography differs from Cooking Lake by the greater number and irregularity of the lakes. Four separate basins occupied by muskegs were examined in this district.

No. 1 is a small area near Looma, not more than 200 yds. in diameter, similar in general topography to No. 1 previously described from the Cooking Lake district, but presenting more strongly marked features of retrogression.

The dominant plant is *Ledum groenlandicum*, but this is tending to die out, particularly in certain spots, as will be described later. Accompanying

plants in the order of their abundance are: *Eriophorum vaginatum* Torr., *Vaccinium canadense* Kalm., *Cladonia rangiferina* Web., *Vagnera trifolia* (L.) Morung, *Polytrichum commune* L., *Rubus chamaemorus* L., *Vaccinium vitis idaea* L. *Vaccinium oxycoccus* is only represented by occasional isolated plants and from the authors' knowledge of this muskeg the relative quantity of this plant seems to have decreased during the last five years. On the other hand, *Cladonia* is increasing and is invading both *Sphagnum* and *Polytrichum* patches.

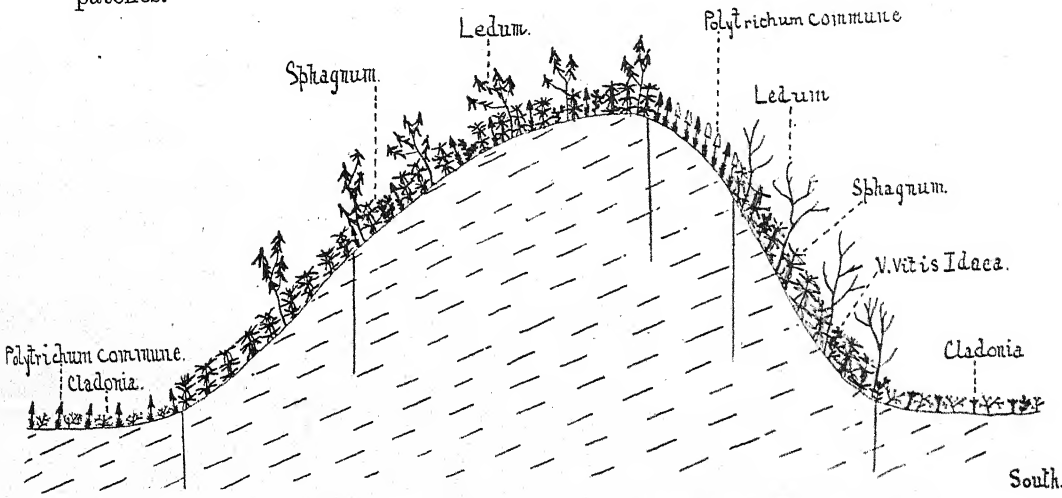


FIG. 2. Sphagnum mound, showing dying back of vegetation on S. facing slope. Vegetation in black is living, in outline dead. No. 1 Muskeg, Looma district.

The appearance of a mound in this muskeg is illustrated in Fig. 2. It shows that these mounds, which cover the surface, while built up by the original *Sphagnum* covering, are now being invaded by a different type of vegetation, particularly on the slopes facing the south. Because of this the appearance of the muskeg is entirely different according to whether it is viewed from the south or the north. Viewed from the north the mounds appear to be covered with a good growth of *Sphagnum* and *Ledum*. From the south they appear brownish in colour, being covered with dead *Polytrichum commune* and dead *Ledum*, only the lower slopes of the south face having a slight growth of *Sphagnum*. The depressions between the mounds are covered chiefly with *Cladonia rangiferina*. A border of *Carex* bog surrounds the muskeg, this being invaded at the outer edge by willow scrub.

In comparing the *p*H concentration of the waters from the marginal *Carex* bog and the muskeg itself there is found a steep gradient from salinity to a strongly acid reaction. The *p*H concentration of the water in the *Carex* bog is 7·5 and this remains constant to within 2 ft. of the edge of the muskeg. The water squeezed from the living *Sphagnum* on the north side of the mounds is *p*H 4·5.

No. 2. The general features of this small area are illustrated in Fig. 3. The surface of the muskeg is covered with mounds formed of *Sphagnum* peat but no living *Sphagnum* occurs except small isolated patches on the north face of a few of the mounds. The original flora appears to have been similar to No. 1 muskeg near Cooking Lake but progressive desiccation has caused an entirely different aspect. *Ledum groenlandicum* and *Sphagnum* were originally the dominant plants, but hardly a living plant is now to be found, although the surface is covered with dead branches. The living plants now consist of *Vaccinium canadense*, *V. vitis idaea*, *V. oxycoccus* (very rare), *Cladonia rangiferina* (scarce) and *Polytrichum commune*. This feature of retrogression is probably due to the exceedingly small size of this muskeg, the actual diameter being 200 ft.

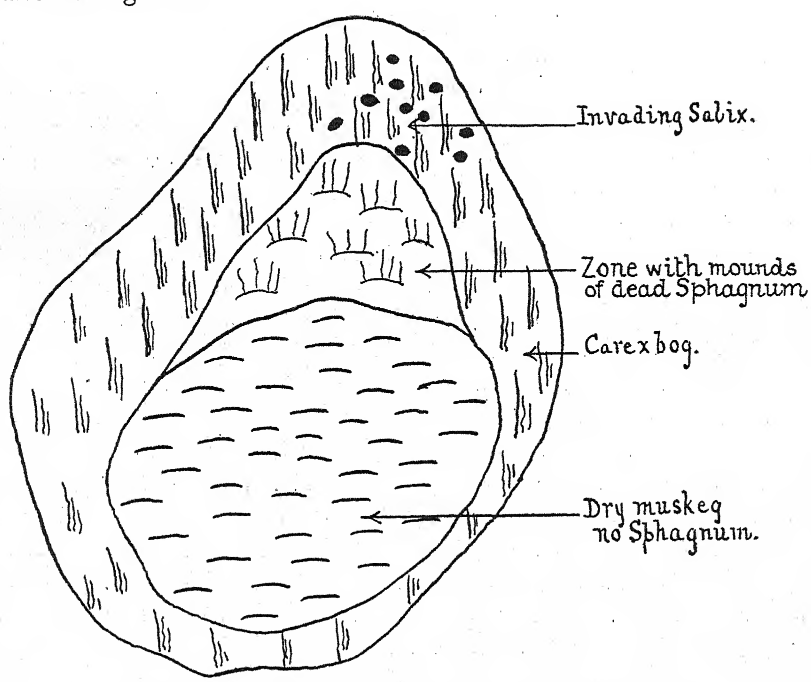


FIG. 3. Topographic sketch of No. 2 Muskeg, Looma district.

The *Carex* border averages about 30 ft. in width and in some places is being invaded by *Salix*. Between the north side of the muskeg and the *Carex* bog lies an intermediate zone showing mounds of *Sphagnum* peat, dead and much disintegrated and isolated patches of dead *Ledum*. The only living vegetation are plants which have immigrated from the surrounding poplar parkland. A complete list is as follows: *Epilobium angustifolium* Roth., *Lonicera involucrata* (Richards) Banks, *Equisetum sylvaticum* L., *Rubus arcticus* L., *Cornus canadensis* L., *Tussilago farfara* L., *Ribes* sp., *Salix* spp., *Populus tremuloides* (seedlings), *Carex canescens* L., *Calamagrostis canadensis* (Michx.) Beauv.

No. 3 is an example of extreme retrogression, the original muskeg having completely disappeared. The basin was originally even smaller than the one just described and the last vestige is now represented by small patches with isolated plants of *Ledum* and *Vaccinium vitis idaea*. On the small mounds (originally tenanted by *Sphagnum*) are now to be found many grasses, *Epilobium angustifolium*, *Equisetum sylvaticum*, and in the hollows between the mounds are *Rubus arcticus*, *Ribes* spp., *Potentilla comarum*, *P. monspeliensis*.

The *p*H of the water between the mounds was 6·0.

Other small peat areas in this district showed similar features; generally speaking the greatest evidence of retrogression due to desiccation is seen in the smaller muskegs.

THE STONY PLAIN MUSKEG

Large areas of the country to the west of Edmonton consist of muskeg. The region that has been particularly studied lies on the north side of the Saskatchewan River within a thirty mile radius of Edmonton. The long stretches of muskeg country in this district contrast sharply with the small isolated basins that are so plentiful to the east.

Passing westward from Winterburn (see Map) the main road rises over a lobe of plateau land at the 2300 ft. level covered with morainic deposits, and at Spruce Grove skirts the southern edge of the Sturgeon Valley which is marked out on the map by stippling—light between 2300 ft. and 2200 ft. and dark below 2200 ft., where there is an interrupted strip of muskeg in some places and fairly large white spruce in others growing on old muskeg ground. Our field observations show that during the retreat of the ice-sheet this part of the Sturgeon Valley was occupied by a lake, which at first was held up to the 2300 ft. contour line by an ice-lobe which filled the lower part of the valley of which Big Lake is now the centre. During this period the ice in the lower part of the valley dammed the outlet, and the head of the valley north of Stony Plain became filled with a marginal lake in which was deposited fine glacial silt, laid down as a marginal deposit below the 2300 ft. level. Subsequently, as the ice retreated, the valley became partly drained through the gorge now extending from St Albert to Sunny Glyde, Big Lake still remaining as the last remnant of this post-glacial lake.

The muskegs here, in spite of evident signs of retrogression, have not suffered so much from desiccation as those in the east, and this feature may be due to their larger size. They usually have a thick stand of *Picea mariana*, *Larix laricina* and *Betula papyrifera*, thus approaching more closely to the climax type. This is particularly noticeable at the margin, where they are usually bordered with a fringe of taller trees, so that from a height of land one may see, over the lower country in the distance, long stretches of muskeg covered by small trees, with a border of tall black spruce that stands out against the horizon.

Phot. 4. Forest of *Picea mariana* with *Ledum groenlandicum* at the west end of the Stony Plain muskeg (p. 327).

Phot. 5. West end of Stony Plain muskeg. Muskeg on the right, with *Picea mariana*, *Ledum* and *Sphagnum*. *Scirpus* bog on the left (p. 327).

An area about three-quarters of a mile long and one-third of a mile wide at the south-western edge of this post-glacial lake shelf has been studied in detail, and retrogressive changes of great interest due to the inflow of springs highly charged with mineral salts will be described. The muskeg is bounded on each of the three sides by rising ground, tenanted by large trees of *Picea albertiana* S. Brown coming from the parkland vegetation. A study of many of these borders seems to show that this tree flourishes particularly well on the decomposed peat of the margin of receding muskegs if the margin is well drained. The outstanding feature of this area is a lake (Plate VIII, Phots. 6–8), which, instead of representing a stage of upbuilding of the muskeg, is clearly encroaching upon it.

A plan of the general appearance of the area is shown in Fig. 4. The features presented by the numerous island outliers of mature tree-clad muskeg at the west end of the lake, and the character of the muskeg banks of the lake, at once suggested that the lake represented a stage of retrogression. It was not, however, until hydrogen ion concentration measurements of the lake and muskeg water were taken, borings over the lake bed and muskeg were carried out, and the dying back of *Sphagnum* near the lake and the presence of calcium salts in the peat noted, that this view became conclusive.

An account may first be given of the vegetation units of muskeg and *Carex-Scirpus* bog.

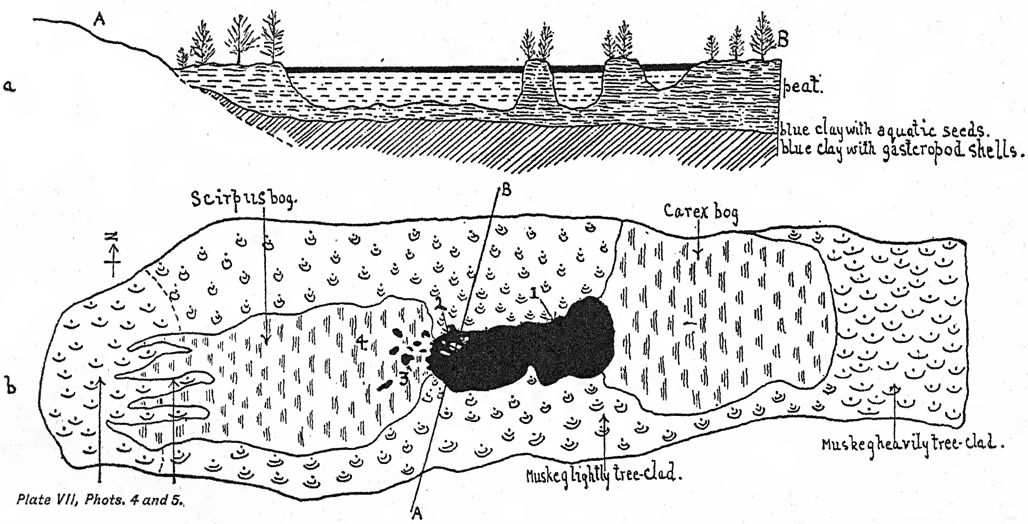


FIG. 4. Muskeg near Stony Plain. (*a*) Section along line A, B in plan, (*b*) showing calcareous lake occupying basin of decomposed peat with islands of peat still surviving. The numbers 1–4 indicate spots from which the water has been analysed (see p. 333).

THE MUSKEG AREA.

The dominant tree is *Picea mariana* (Mill) B.S.P. associated with *Larix laricina* and *Betula papyrifera*. The western and eastern ends are more heavily

tree clad (Fig. 4) and the muskeg is less denuded and more closely covered with vegetation. This is illustrated by Pl. VII, Phot. 4 and Pl. IX, Phot. 9.

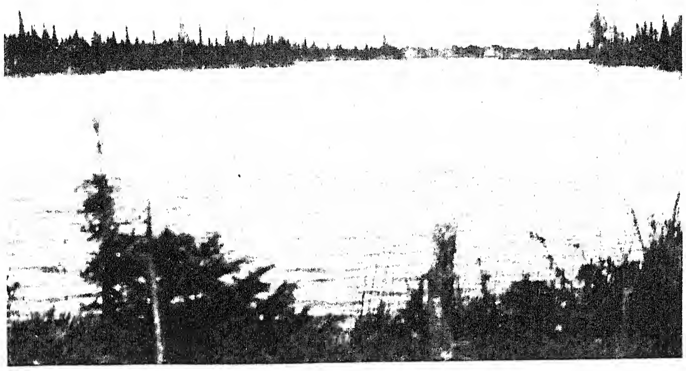
The ground vegetation is composed of the following typical peat-forming plants which are here arranged in order of their relative abundance: *Ledum groenlandicum* Oedr., *Sphagnum acutifolium*, *Empetrum nigrum* L., *Hypnum* spp., *Vaccinium oxycoccus* L., *V. vitis idaea* L., *Drosera rotundifolia* L., *D. linearis* Goldie, *Rubus chamaemorus* L., *R. arcticus* L., *Vagnera longifolia* L. (Morung). With these plants, and particularly under the trees or near the margin of the lake, occur *Pyrola uliginosa*, *Orchis rotundifolia* Pursh, *Corallorhiza wisteriana* Conrad. On the more lightly wooded parts of the muskeg occur plants which suggest retrogressive changes, such as *Salix candida*, *Lonicera involucrata*, *Epilobium angustifolium* L., *Limnorchis dilatata* (Pursh) Ryd., *Cladonia rangiferina*, the latter being more abundant where the trees thin out.

Throughout the muskeg there are clear signs that retrogression is taking place, for the *Sphagnum* forming the familiar mounds on our muskegs is frequently dead towards the base, or in patches on the sides of the mound, and these are invaded by blue-green algae. When decomposition has proceeded for some time such dead patches become replaced by *Hypnum*, and it is not uncommon to see a partly decomposed *Sphagnum* mound made up of smooth patches of peat covered with blue-green algae, while other patches show a close sward of *Hypnum*. Tests carried out in the field showed a strong reaction for carbonates with dilute hydrochloric acid, a reaction not given when the reagent is used on the living *Sphagnum*.

The islands in the lake (Pl. VIII, Phot. 8) have essentially the same flora, save that *Sphagnum* is replaced to a great extent by *Hypnum*. This type of vegetation changes very little until the edge of the lake is approached when species of *Scirpus* and *Carex* with *Elephantella groenlandica* (Retz.) Ryd., *Parnassia palustris* L., *P. glutinosa* Pers., *Lonicera involucrata*, *Triglochim maritimum* L., form a narrow irregular fringe about 18 in. wide (Pl. VIII, Phot. 7).

It was not found possible to cut sections through the peat on account of the amount of water coming through, but borings with a 2 in. clay auger and 25 ft. extension rods were carried out in several spots of the muskeg, both within a few yards of the lake and near the margin of the area. All these borings agreed in showing a depth of 13 ft. underlain by stiff blue clay. *Sphagnum* appeared to be abundant in the peat to within a few inches of the bottom and the auger passed through the remains of tree trunks to within a few inches of the base of the peat. A thin layer at the base of the peat contains no *Sphagnum* and is made up of the remains of *Scirpus*.

The blue clay was bored through to a depth of 4 ft. or 5 ft. in various sections. It appeared to be uniform in character, containing very little water, with numerous quartz grains, generally less than 1 mm. in diameter. It quickly dries into a hard substance only fractured with difficulty. The upper



Phot. 6. Calcareous lake on the Stony Plain muskeg (cf. Fig. 4, p. 327).

Phot. 7. Stony Plain muskeg. Border of *Carex* and *Scirpus* on the lake bank (p. 328).

Phot. 8. Muskeg islands in the lake on the Stony Plain muskeg (p. 328).

layers contain numerous seeds or fruits of the following plants: *Hippuris vulgaris* L., *Potamogeton obtusifolius* Mert and Koch, *Potamogeton* sp., *Cyperus* sp., *Scirpus subterminalis* Torr. The remains of these aquatic plants appear to be confined to the upper 3 or 4 in. of the clay, at lower depths the very small shells of gastropods are exceedingly abundant to a depth of 4 to 5 ft. This gave a total depth (peat and clay) of 18 ft. from the surface, and was as far as it was possible for the boring equipment to penetrate owing to the exceeding stiffness of the clay. Mr J. A. Kelso, Director of the Industrial Laboratories, kindly had an analysis made of this clay, the result of which is given below.

Silica	62·2 %
Alumina	10·1
Iron oxide	3·1
Lime	7·6
Magnesia	1·4
Sulphates	nil
Phosphates (P_2O_5)	0·1
Ignition loss	14·4
Alkalies, etc.	1·1

Dr J. A. Allan, Professor of Geology, to whom we are indebted for an examination of the clay, reports that the material is a pure glacial silty clay deposited near the retreating ice-point. A similar clay occurs in the small basins between morainic ridges and mounds in the Cooking Lake and Looma districts and it is upon this impervious stiff glacial clay that all the peat deposits appear to rest, a matter of some interest, since it gives evidence that the peat bogs here described began to grow immediately after the last ice-sheet retreated from this country. This clay will be referred to later when dealing with the post-glacial history of this region.

Carex and *Scirpus* Bog.

Reference to Fig. 4 will show this extending as two irregular areas from the east and west end of the lake. At the west end the *Scirpus* runs into the muskeg as a series of winding channels, the boundary between these and the muskeg being exceedingly sharp as is shown in Pl. VII, Phot. 5. The muskeg dominated by *Ledum* and *Sphagnum* is seen on the right, the boundary resembling the bank of a stream formed of *Sphagnum*, the depressed *Scirpus* bog representing the stream.

The vegetation of the east end of the bog consists of *Carex aquatilis* Wahl., *C. stricta* Lam., *C. prairea* Dewey, *Eleocharis palustris* (L.) R. and S., *Juncus stygius* L., *Scirpus caespitosus* L., *Calamagrostis confinis* (Willd.) Nutt., *Cornus canadensis* L., *Tofieldia glutinosa* Pers. During the earlier part of the summer the water lies to a depth of 3 or 4 in. between the tufts of vegetation and becomes filled with a growth of *Utricularia intermedia* Hayne. Amongst this *Carex* bog occur mounds of muskeg vegetation varying in size from a few inches to a few feet across and rising about 6 in. above the level of the bog. These last traces of the muskeg vegetation amongst the *Carex* show various phases of retrogression from stages where there is still much *Sphagnum*

and where *Ledum* is the dominant plant, to others where the *Sphagnum* has been entirely replaced by *Hypnum* and the *Ledum* partly by species of *Salix*, whilst *Elephantella groenlandica* (Retz.) Ryd., is invading the margin of the mound. Small trees, some dead and others barely living, frequently cap the summits of these little mounds. The area of *Scirpus* bog west of the lake, particularly the long strips which run into the muskeg (Fig. 4, also Pl. VII, Phot. 5) frequently bear both larch and spruce, either singly or in patches; such trees are always stunted, partly defoliated or dead. They, like the muskeg mounds, must be regarded as part of the relict flora of the muskeg which formerly extended over these areas.

At the west end of the lake the vegetation is characterised by the following, in order of abundance: *Scirpus caespitosus* L., *S. pauciflorus* Lightf., *Juncus stygius* L., *Eleocharis acuminata* (Muhl) Nees, *Calamagrostis confinis*, *Carex aquatilis* Wahl., *C. stricta* Lam., *C. prairea* Dewey, *C. aurea* Nutt., *Triglochin palustre* L., *Tofieldia palustris* Huds., *Galium tinctorum*, *Limnorchis dilatata* (Pursh) Ryd.

Much of the valley bears a vegetation which is so much afloat that care has to be taken in walking over it not to break through. Borings were taken over this area both at the eastern and western end of the lake. All of them showed 13–15 ft. of peat which (below the surface liquid peat) contains abundance of *Sphagnum* down to the base, which rests on the same blue clay crowded with gastropod shells. There is then clear proof that the *Carex* and *Scirpus* bog at each end of the lake is a later invasion of these areas—originally muskeg—by the type of vegetation dominated by sedges, rushes and grasses, with other monocotyledons.

In the next section of this paper the degree of alkalinity or acidity of the water in the muskeg, in the *Carex* and *Scirpus* areas and in the lake are recorded (p. 333); the results of the analyses of samples of lake water are tabulated (p. 333); and the rate of tree growth on the muskegs is graphed (pp. 339–40).

The Lake and Drainage Waters.

Seen during the summer, the waters of the lake are clear to a depth of about 6 in.; below this the water is filled with a greyish to pink deposit and this extends to a depth of about 9 ft. The muskeg banks, which are about 1 ft. above the water, go down abruptly, but during the summer it was not possible to investigate the lake or to reach any of the islands. During November, December and January the whole area is frozen and the lake covered with 2 ft. of ice, and it was during this period that borings were taken over the whole area through holes cut in the ice.

All the borings agree in showing that peat underlies the whole lake. The floor is uneven, but the average depth at which the peat is reached below the surface of the lake is 8–9½ ft. The depth from the surface of the lake to the

underlying blue clay (which is of exactly the same character as that underlying the adjacent muskeg, *Scirpus*, and *Carex* bog) is 13 ft. The lake then rests upon peat of an average thickness of $4\frac{1}{2}$ ft.; this is composed very largely of *Sphagnum* and is therefore an extension of the lower layers of the surrounding muskeg under the lake.

Great interest attaches to the borings taken on the small muskeg islands so numerous at the west end of the lake. In all cases *Sphagnum* peat extended down continuously from the surface to within a few inches of the clay floor 13 ft. below. These islands may be described as pillars of peat standing in the lake.

The spongy deposit filling up the lake to within about 6 in. of the surface is a peculiar algal colony which has attained the depth of about 8 ft., where it overlies the peat. Over its surface is spread a crust made up of pink flakes a few inches in diameter, curled up at the edges to reveal a blue-green under surface. This surface layer is richer in blue-green algae than is the rest of the deposit. When this is skimmed off there is exposed a pink substratum smelling strongly of hydrogen sulphide. It is made up of soft nodules forming a porridgy mass which can be stirred up with a stick. In it is embedded a large quantity of *Chara*, and near the border *Utricularia* is abundant. As is shown below, it is particularly rich in diatoms and unicellular green algae.

Various collections of this material were made and brought back to the laboratory for examination. It soon became evident that the deposit was an extremely rich algal growth. Material collected during September and October was sent to Mr C. W. Lowe, M.Sc., of the University of Manitoba, who kindly consented to examine it and we are much indebted to him for the following extensive list of algae from this deposit.

Collection No. 1 was taken from the crust already mentioned overlying the deposit, collections No. 2, 3 and 4 from the deposit itself. No. 2 was from the west end of the lake in September; No. 3 from near the centre during November; No. 4 from a smaller lake on the *Scirpus* bog. Nos. 5 and 6 are from submerged vegetation along the margin, the former growing on *Hypnum*, the latter on *Utricularia*. Sample No. 7 contained a mass of a fresh-water sponge, either *Spongilla fragilis* or *Spongilla lacustris*.

LIST OF ALGAE.

Myxophyceae	1	2	3	4	5	6
Chroococcus turgidus (Kütz.) Näg.	+	.	+	.	.	+
C. limneticus Lemm.	.	.	.	.	.	+
C. macrococcus (Kütz.) Raben.	+	.	.	.	.	.
Gloecocapsa fusco-lutea (Näg.) Kütz.	.	+	.	.	.	.
Aphanothece saxicola Näg.	+	.	.	.	.	.
Microcystis sp.	+	.	.	.	.	.
Gomphosphaeria aponina Kütz.	+	.	.	.	+	+
Coelosphaerium kützingianum Näg.	+	.	+	.	+	+
Merismopedium tenuissimum Lemm.	+	.	+	.	+	.
Lyngbya aerugineo-caerulea (Kütz.) Gomont. ...	.	.	.	.	+	.
Stigonema minutum (Ag.) Hass.	.	.	.	.	.	+
Also fragments of *Oscillatoria, Rivularia, Nostoc* and *Anabaena*	+	.	.	.	+	+

LIST OF ALGAE (*continued*).

	1	2	3	4	5	6
Bacillarieae						
Amphora ovalis Kütz.	+	.	+	.	+	.
Cymbella cymbiformis Ehr.	.	+	+	.	+	+
C. cymbiforma parva (W.Sm.) H.V.H.	.	.	+	.	.	.
C. gastroides Kütz. forma minor H.V.H.	.	.	.	+	.	.
C. ehrenbergii Kütz.	+	.	+	.	.	.
C. lanceolata Ehr.	+	.	+	.	.	.
Stauroneis phoenicenteron Ehr.	+	.	+	.	.	+
Navicula viridis Kütz.	+	.	+	.	+	.
N. oblonga Kütz.	+	.	+	.	.	+
N. radiosa Kütz.	.	.	+	.	.	.
N. radiosa var. acuta (W.Sm.) H.V.H.	.	.	+	.	.	.
N. cuspidata Kütz.	.	.	+	.	.	.
N. sphaerophora Kütz.	+	.	+	.	.	.
N. iridis Ehr.	.	.	+	+	.	.
N. iridis var. producta H.V.H.	.	.	+	+	.	.
Gomphonema constrictum Ehr.	.	.	+	.	.	+
G. intricatum Kütz.	+	.	+	.	.	.
Epithemia turgida (Ehr.) Kütz.	+	.	+	.	.	+
E. argus Kütz.	+	.	+	.	.	+
Rhopalodia gibba (Kütz.) O. Müll.	+	.	+	.	.	+
Synedra ulna (Nitzsch.) Ehr.	+	.	+	.	.	.
S. ulna var. splendens (Kütz.) H.V.H.	+	.	.	.	.	+
Fragilaria crotonensis (A.M.Edw.) Kitton	.	.	+	.	.	.
F. capucina Desmaz.	.	.	.	.	.	+
Surirella sp?	.	.	+	.	.	.
Hantzschia amphioxys (Ehr.) Grun.	.	.	+	.	.	+
H. amphioxys var. elongata H.V.H.	+	.	+	.	+	.
Chlorophyceae						
Oocystis solitaria Wittr.	+	.	.	.	.	.
Tetraedron minimum (A.Br.) Hangs.	.	.	.	.	+	.
Scenedesmus quadricauda (Turp.) Bréb.	+	+	+	+	+	+
Coelastrum microporum Näg.	.	.	.	.	.	+
Pediastrum tetras (Ehr.) Ralfs	.	.	+	.	+	.
P. boryanum (Turp.) Menegh.	+	.	.	+	+	.
Cylindrocapsa conferta W.West	+	.	.	.	.	.
Spirogyra (not in conjugation)	.	.	.	.	.	+
Euastrum dubium Näg.	.	+	.	+	.	.
E. insulare (Wittr.) Roy.	+	.	.	.	.	.
Cosmarium granatum Bréb.	+	+	+	+	+	+
C. rectangulare Grun.	+	.	.	.	.	+
C. impressulum Elfv.	+	.	.	.	.	+
C. laeve Raben.	.	.	.	+	.	.
C. pokornyanum (Grun.) W.W. and G.S.W. ...	.	.	.	.	.	+
C. hammeri Reinsch.	.	.	.	.	.	+
C. quadrum Lund.	.	.	.	.	.	+
C. humile (Gay) Nordst. var striatum (Boldt) Schm.	+	.	.	.	.	+
C. subcucumis Schm.	.	.	.	.	.	+
C. reniforme (Ralfs) Archer	+	.	.	.	.	.
C. subcrenatum Hantz.	+	.	.	+	+	.
C. botrytis (Bory) Menegh.	+	.	.	.	.	+
C. margaritaceum (Lund) Roy and Bissett ...	+	.	.	.	.	.
Staurastrum muticum Bréb.	+	+	.	.	.	.
S. polymorphum Bréb.	.	.	.	+	.	.
S. alternans Bréb.	+	.	.	.	.	.
S. paradoxum Meyen	+	+	.	.	.	.
Bulbochaete sp? (Not in fruit)	.	.	+	.	.	.
Ophiocytium cochleare (Eichw.) A.Br.	+	.	.	.	.	.

Chara is also an important member of this lake flora. It occurs at the surface of the lake, particularly at the western end, in considerable abundance and is met with living in the upper layers of the calcareous deposit in the lake. Its remains can be recognised amongst the calcareous deposit at much greater

depths. Mr James Groves has kindly examined the material and has informed us that the species is *Chara contraria* with numerous root bulbils—the first instance of root bulbils found in this species.

REACTION AND ANALYSIS OF WATER.

We have, then, a calcareous lake with clear surface water and 9 ft. of calcareous material below resting on a floor of peat bounded by banks of peat.

There being no stream either flowing into or out of this lake the level must be maintained by underground springs, which, as the evaporation from the surface during the hot summer months is considerable, and as the level does not noticeably vary, must be of just sufficient flow to replace evaporation.

The acidity or alkalinity of the waters of the lake, the water on the surface of the *Carex* bog, and the water held in the masses of *Sphagnum* on the muskeg area have been measured in the field by means of pH indicators, the values so obtained being as follows:

Muskeg area.	Water squeezed from living *Sphagnum*	pH	4·5
Carex bog.	Water from surface between tufts of vegetation	pH	7·5
Lake.	Water from surface layers	pH	9

That the lake water with a pH value as high as 9 should be bounded by banks of peat with *Sphagnum* having a pH of 4·5 shows quite clearly—even without the observations concerning the substratum—that the lake must represent a retrogressive rather than a progressive stage in the history of this muskeg region.

Certain indications point to the western end of the area as the place of outlet of the springs feeding the lake. The *Scirpus* bog at the western end is more obviously afloat than the *Carex* bog at the eastern end, while at the same time the eastern end is somewhat firmer but bears more water on the surface.

In order to see whether there is any marked difference in the water from different regions, samples have been taken from four different spots which are marked 1, 2, 3, 4 respectively in Fig. 4. No. 1 sample was taken from the surface water about 2 ft. from the bank, No. 2, 3 ft. from the bank of a small bay. No. 3 from one of the numerous small pools which break the surface of the floating *Scirpus* bog. No. 4 was obtained by cutting away the floating mat of *Scirpus* and obtaining the sample from below. The analyses of these samples were carried out by the Provincial Industrial Laboratories and the results are as follows:

Parts per Million.

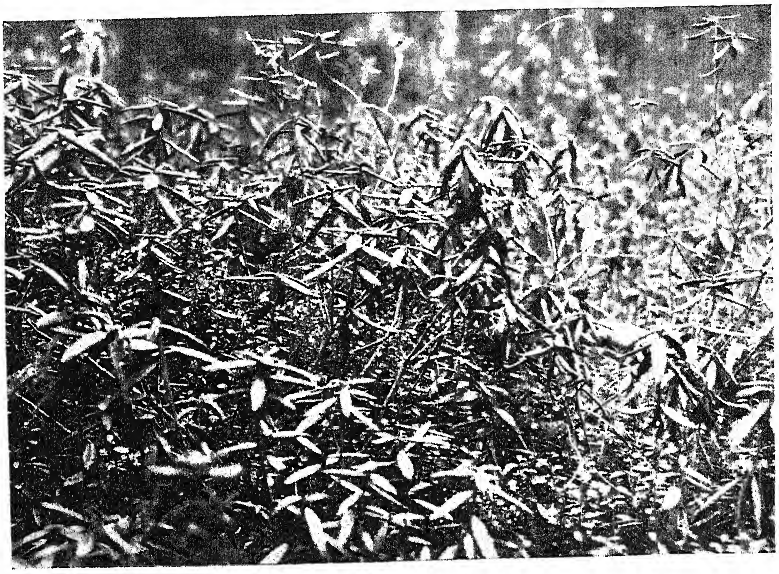
	No. 1	No. 2	No. 3	No. 4
Calcium	53·0	61·8	78·2	86·1
Magnesium	25·8	29·6	41·2	39·2
Sodium	4·0	6·5	5·2	9·6
Sulphates (SO_3)	53·9	61·8	44·2	60·0
Carbonates (CO_2)	102·3	103·9	185·7	181·1
Silica	0·4	0·2	0·4	0·4
Iron Oxide and Alumina	nil	nil	nil	nil
Vegetable Matter	99·0	82·0	42·3	58·0
Total Solids	355·3	383·6	413·9	461·0

The progressive increase of mineral salts in solution, particularly of calcium carbonate and magnesium carbonate, as one passes from the east end of the lake to the *Scirpus* bog at the western end suggests that the springs feeding the lake have their outlet in the western region of the area and this is borne out by the curious winding channels of *Scirpus* bog which intersect the muskeg in this region.

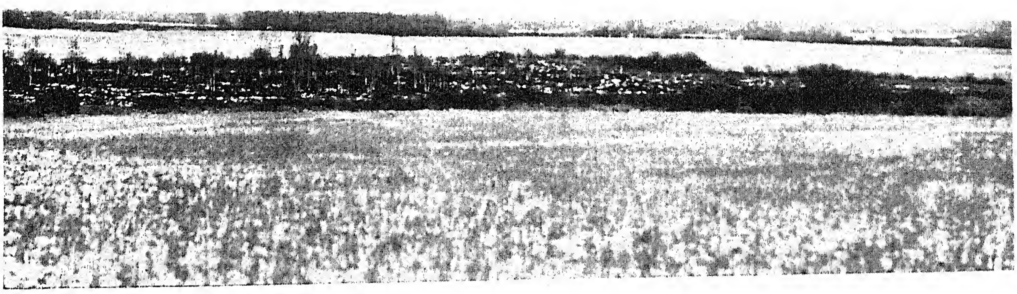
The tests of the H-ion concentrations and the collection of water samples were made in the autumn before the area became frozen. Measurements of the rate of growth of trees from this and other muskegs have been carried out and these are described in a later section of this paper.

It seems clear from the features described here that the muskeg began its history during the retreat of the ice-lobe from the Sturgeon basin. The nature of the clay and the presence of gastropods indicate the presence of an early post-glacial lake, the seeds and fruits of aquatic plants in the upper layers representing the primary free-floating vegetation of this lake. By the action of the overflow stream cutting through the glacial deposits blocking the trench between St Albert and Sunny Glyde (see Map), the level of the lake became progressively lowered, leaving the border of fine clay exposed, and upon this a vegetation composed of sedges and rushes succeeded the free-floating vegetation of the former lake. Not very much peat appeared to be formed by the *Carex* bog, but when *Sphagnum* and accompanying peat-forming plants spread, the subsequent growth of the muskeg must have been continuous until about 12–13 ft. of peat was formed—probably representing, in this northern climate with a short growing season, a considerable length of time. At length springs rich in calcium sulphate, calcium carbonate and magnesium carbonate broke out where the lake now stands. Springs as rich in calcium and magnesium salts as the water analyses show would certainly stop the further growth of *Sphagnum* and other peat-forming plants. As a result the bare peat would be exposed and water from the springs would collect in hollows on the surface of the peat bog. The exposure of a bare peat surface, the presence of organisms setting up decomposition in the peat, and mineral salts in considerable concentration, might be expected to produce in time a basin, which, owing to the causes mentioned, would tend to widen and deepen. The algae and *Chara* present in such enormous abundance are the chief agents responsible for the great precipitation of mineral salts above the floor of the lake.

Such curious retrogressive changes in peat deposits are not in the authors' experience common, although the breaking out of springs richly charged with mineral salts is not uncommon, particularly in the country west of Edmonton. In a ravine coming into the Saskatchewan Valley a few miles west of Edmonton springs have formed a tufa deposit of considerable thickness and the decomposition of an adjacent small peat bog may be due to the percolation from such springs. Another peat deposit a few miles north of Stony Plain



PHOT. 9. *Ledum groenlandicum* and *Empetrum nigrum*. West end of Stony Plain muskeg.



PHOT. 10. Muskeg surrounded by ground cleared of poplar woodland and now planted with oats. Dec. 1925 (see p. 335).

near Calahoo, on the same line of muskeg country, exhibits a somewhat similar feature, although owing to the thinness of the peat deposit only a shallow basin has been formed, the floor of which is covered with calcareous marl. Owing to the area occurring on a slope, the hollow is not permanently filled with water and the algal deposit is therefore dried up except during the early part of the summer. These other cases have not been investigated in detail, and are only quoted here as a suggestion that the features recorded may not be uncommon on muskegs situated on the Edmonton geological horizon.

RETROGRESSION DUE TO CLIMATIC FACTORS AND FIRE

Peat bogs in the parkland belt generally show distinct stages in retrogression, and the type of vegetation is now markedly different from the abundance of *Sphagnum* that must have characterised these areas at the period of their maximum growth. In the southern region of the parkland and Edmonton district the muskegs tend to be confined to small basins frequently only a few hundred yards or less in diameter, and stand as islands of peat bog vegetation in the surrounding poplar woodland. Large continuous areas of peat are not usually met with until the northern coniferous forest is reached. Generally speaking the evidences for retrogression are more marked in the south although the actual size of the basin is obviously a contributing factor. An average annual precipitation varying from 12 in. to 22 in. and a growing season of only four months in the year are not conditions which might be expected to favour the formation of extensive peat deposits. Evidences of the curiously localised condition of these peat areas and the abrupt changes of vegetation at their margin are frequent, and an interesting example is shown in Pl. IX, Phot. 10. Here the muskeg originally lay as a narrow winding strip in poplar woodland. The woodland has been cleared and the ground (black soil) cultivated. The photograph shows the stubble of an oatfield passing up to the edge of the narrow fringing *Carex* surrounding the muskeg. Living *Sphagnum* may be absent on such a peat bog at the present time although the peat below is formed very largely of this moss.

The origin of the muskegs must be sought in small lakes which dotted the morainic areas of the parkland after the recession of the ice, the flora of the lakes being represented by the seeds and fruits of aquatic plants from the surface of the blue clay underlying some of the areas described in this paper. From that period to the stage when the muskegs began to show retrogression, their history appears to be one of uninterrupted upbuilding by *Sphagnum*, and small trees of black spruce and larch seem to have been present throughout this stage. How long the retrogression period has lasted and how far the stages have been accelerated by fire and later by man's influence we have at present no evidence to show. The retrogression stages are probably slow compared with those which might take place in a country

with an open winter such as north-western Europe, for in this region the surface is usually frozen for seven months in the year.

The dying back of *Sphagnum* seen on the south facing slopes of the mounds on some muskegs appears to suggest decreased precipitation and increased evaporation. It is possible that this may be due in part to the immense amount of clearing and draining that has taken place in the parkland belt during the last 40 years. The effect of settlement has been to clear off as much of the natural vegetation cover as possible in order to obtain areas for cultivation and the making of roads and cutting of drains has resulted in a great reduction of surface waters. This is all to the good up to a certain point, since clearing, draining and cultivation undoubtedly reduce the chance of late and early frosts which are a menace to successful cultivation. But in a country with a moderate rainfall and a very high rate of evaporation during the summer months, it may be doubted whether the indiscriminate draining of lakes and all reserves of surface waters is advisable. Many of the larger lakes in the Edmonton district such as Beaver Lake are quite shallow, being not more than 14 ft. in depth. The draining of such lakes is frequently discussed and could be effected without serious difficulty, but such a policy, if completely carried out, would certainly tend to increase aridity.

Another factor that must be considered in regard to retrogression is fire. In a country in which forest fires have been so frequent in the past, it might be expected that very few of the muskegs would have escaped burning over. This may be the case, but on the other hand numerous examples occur like that shown in Pl. X, Phot. 12, where the muskegs are closely covered with symmetrical trees of black spruce. These may be small but growth is slow and such trees are usually about 50 or 60 years old. In a season dry enough to permit burning, spruce in which the branches come to the ground would be highly inflammable, and if not destroyed would certainly retain the marks of burning. There are other muskegs which have clearly been burnt over, an interesting example of this being illustrated in Pl. X, Phot. 11. This little muskeg in the Cooking Lake district is almost circular and not more than 200 ft. in diameter. Remains of burnt black spruce still occur on the surface but the only trees growing at present are birch and poplar which have spread in from the surrounding parkland. No *Sphagnum* occurs and the original muskeg flora is largely replaced by grasses, willows, lichens, and *Vaccinium vitis idaea*. It is difficult to estimate the length of time since burning, but the birches average about 30 years of age and the burning was severe enough to char the surface of the peat, the signs still remaining.

Other cases occur in which the peat has been destroyed to a considerable depth, but this seldom extends over the whole muskeg and frequently mounds and banks occur in areas which were too wet for the fire to enter and where the original muskeg flora still remains but little changed. In some cases where a muskeg area adjoins cleared cultivated land, intentional burning

Phot. 11. Birch and poplar invading a burnt-over muskeg near Cooking Lake. Original vegetation nearly destroyed (p. 336).

Phot. 12. *Ledum groenlandicum* and *Picea mariana* on muskeg in the Cooking Lake district (pp. 322–3).

is carried out and this may proceed for several years and be so thorough as to expose the underlying clay.

The several muskeg areas lying upon the blue glacial clay date back to the period immediately following the recession of the ice-sheet. Fires were more frequent and widespread before the coming of the white man than they are at present as they are now carefully controlled. It must be concluded that if burning was a frequent factor in retrogression the muskegs would not have acquired their present depth of peat. Further, in examples examined by one of us several years ago by means of sections, thin charred layers of peat were present sometimes several feet (4–6 ft.) below the present surface and the peat above the charred layer was formed chiefly of *Sphagnum*. This suggests that at a former period a muskeg could entirely recover its original vegetation after burning; from examples of more recent burning this does not seem to be the case at the present day. The general conclusion we have been led to by our observations is that retrogression occurs to-day from desiccation caused by changed meteorological conditions and the general clearing and draining of the country and that burning, while locally important as producing marked retrogression and even complete destruction of the muskeg, is not responsible for the general shrinkage in growth and change of vegetation so marked in the whole area examined. Muskegs in the central and southern region of the parkland so near prairie must be looked on as relics of a former condition more favourable for peat formation.

THE AGE AND VARYING RATE OF GROWTH OF TREES ON MUSKEGS.

The correlation between the rate of growth of trees and the climatic factor has been a frequent subject of discussion in plant ecology and forestry for a number of years. The most detailed study hitherto made is that by A. E. Douglass[1] on *Sequoia*, Yellow Pine and other trees.

It having been ascertained by us that the trees, although small, are of considerable age, an examination of sections has been made with the object of measuring fluctuations in the rate of growth in former periods and of deciding whether there are any marked differences in muskegs of various types and stages.

With this object sections of trees were taken at a height of about 2 ft. from the ground and for each tree the number of mm. of wood added every ten years (this time period being selected as an arbitrary standard) were measured and recorded graphically. The records show an acceleration of growth in the first 25 years of the life of the tree, which disappears later. This is due not to any climatic factor but to the fact that trees have a higher rate of growth in youth than in maturity. The tree curves discussed here have

[1] **A. E. Douglass.** "Climatic Cycles and Tree Growth." Carnegie Inst. Wash. Publ. 289, 1919. See also **Ellsworth Huntington.** "The Climatic Factor as illustrated in arid America." Carn. Inst. Publ. 192, 1914.

been corrected for this factor according to the method described by Douglass by subtracting the average "Curve of Youth" from each one, and this results in a straightening out of the curve for the first 25 years.

About fifteen trees from the muskeg at Stony Plain were measured, the five shown in Fig. 5 being representative. These all show similar well-marked fluctuations for the last 105 years.

The graphs show two maximum periods of growth, one about 1835, and the other after 1905, while in 1885 there is a period of regression. Every tree without exception shows a maximum growth during 1835. The minimum period 1885 is becoming apparent in some of the trees 10 or 20 years before, but on the whole the agreement is remarkably uniform. All the trees increase their rate of growth after the year 1905 and in some cases after 1865, but during the last 10 years there is a lack of uniformity, for in about a third of the trees measured the growth fell off and in the remainder it increased.

In Cooking Lake Muskeg No. 2, in which the vegetation shows distinct signs of desiccation, trees have been examined which show the same curves as those from Stony Plain. The fluctuations in this muskeg are shown in Fig. 6. As these trees are younger and because the curve for the first 30 years (being partly due to youth) has been omitted, only a few trees go back to the maximum of 1835. The minimum growth period of 1895 and the maximum of the last 20 years correspond perfectly.

These results strongly suggest that in the last 100 years, there were two maximum periods of rainfall—one about 1835 and the other about 1915, and that the period of 1885 was one of drought.

The most remarkable feature shown in these records is the enormous increase in the rate of growth in the trees from Cooking Lake Muskeg No. 2, compared with those from Stony Plain:

Average rate, mm. per year,	Cooking Lake, No. 2	1·13
,, ,, ,, ,,	Stony Plain	0·31

thus showing that the trees on the smaller well-drained muskeg with a more retrogressive type of vegetation are growing about four times as quickly as those on the muskeg which approximates more closely to a climax type.

It has also been observed that the trees of Stony Plain grow at a greater rate towards the east end where the *Sphagnum* is not growing so vigorously. Again, the largest trees are nearly always found along the receding border of the muskeg; as the muskeg has been tree-clad throughout its history, this is not due to invasion taking place from the margin but to an actual increase in growth rate.

The fact that the rate of growth of trees on a muskeg is the converse to the rate of growth of *Sphagnum* is borne out by G. B. Rigg[1] in a study of the growth of trees on the muskegs of the Pacific coast, where he observes that

[1] **G. B. Rigg.** *Bot. Gaz.* **65**, 1918, p. 359.

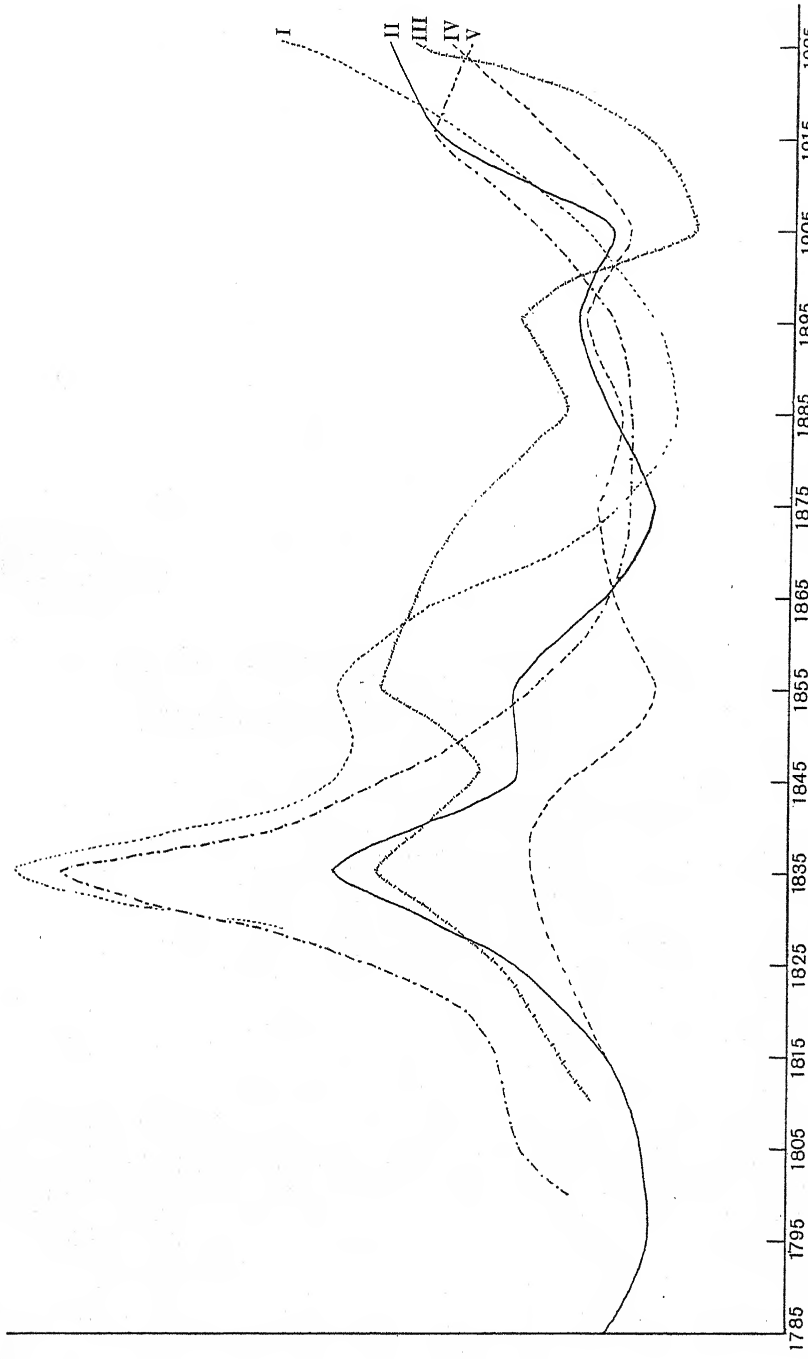


FIG. 5. Graphs showing 10-year increments of five representative trees from Stony Plain Muskeg. The first parts of the graphs are corrected for youth (see text).

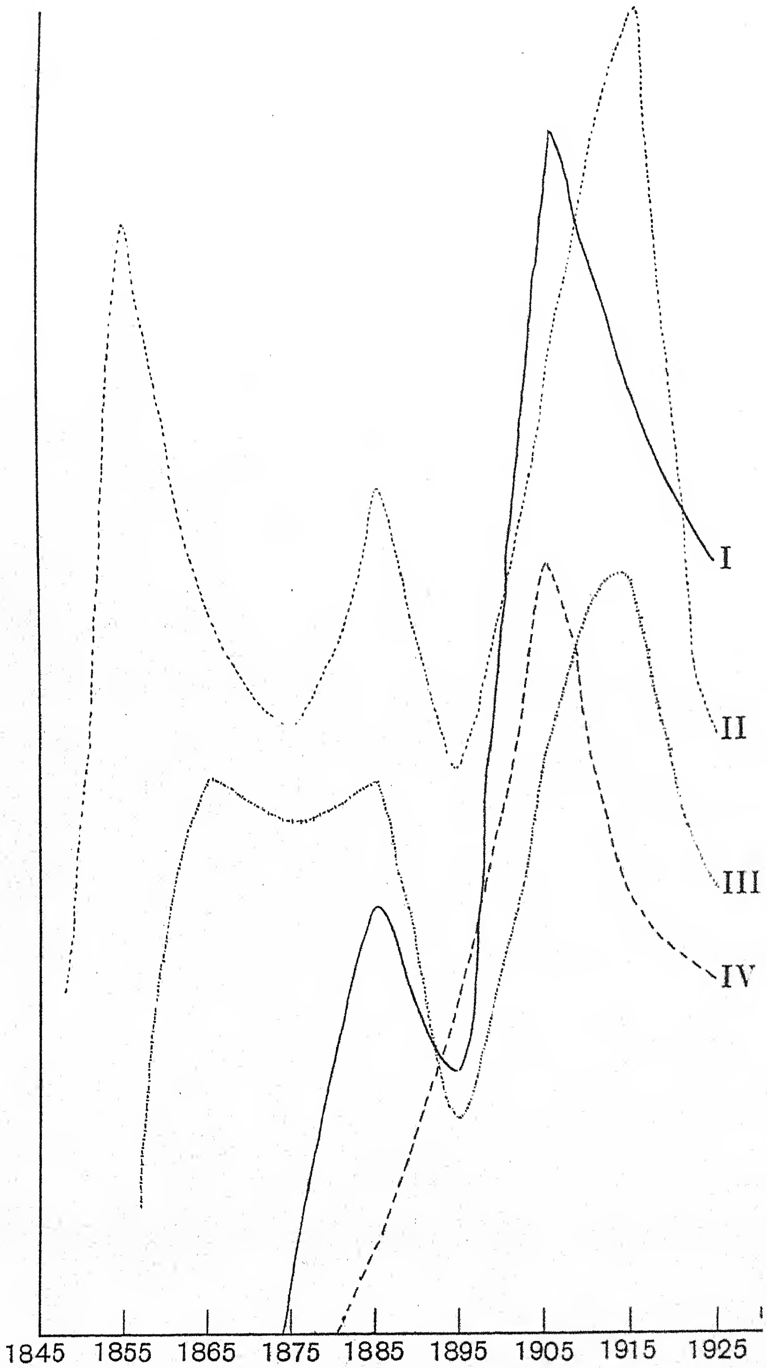


Fig. 6. Graphs of tree-growth from Cooking Lake Muskeg No. 2 (first 30 years of growth not included).

trees are retarded in growth when on actively growing muskegs owing to the toxic influence of the *Sphagnum*.

It would be expected in a muskeg of the type of Cooking Lake No. 2—small, rapidly receding and with *Sphagnum* scanty and in poor condition—that the acidifying effect of the moss would be at a minimum and the conditions for tree growth most favourable. In fact the *p*H of the Cooking Lake muskegs is 5 and Stony Plain *Sphagnum* is 4·5.

SUMMARY.

1. The vegetation, history and retrogressive changes of muskegs in the poplar parkland district of Edmonton are described.

2. *Sphagnum* is tending to disappear and to be replaced by vegetation indicating drier conditions and a cessation of peat-formation.

3. These muskegs are formed on fine glacial clay in small basins in morainic regions. Seeds of aquatic plants are present in the surface layers of the clay, which is covered with a few inches of *Scirpus* peat. *Sphagnum* has dominated the muskegs until more recent times.

4. Retrogressions due to fire, desiccation and the inflow of springs highly charged with mineral matter, causing the formation of a calcareous lake in a peat basin, are described.

THE SALT MARSH VEGETATION OF LITTLE ISLAND, Co. CORK

By R. H. McCREA, B.Sc.

(*With one Figure in the Text.*)

The following ecological study, with the exception of the chemical analyses, was made during a holiday in August, 1924.

Little Island is situated in the tidal part of the River Lee, roughly half-way between Cork and Queenstown. *Fucus* and *Enteromorpha* grow in abundance on its shores. It is at the present time not really an island but a peninsula, being joined to the mainland by more or less swampy meadows, through which drains are cut, and from which the high tides are excluded by means of dams and sluice-gates. It appears, from local information, that the date of reclamation can be fixed approximately at three-quarters of a century ago.

The "island" consisted at that time of four distinct islands, the intervening land between these having been reclaimed and preserved in much the same way. These reclaimed lands are shown as shaded regions in Fig. 1.

It is these features which lend special interest to the flora of the locality, as various stages in its development can be traced from the typical salt-marsh vegetation, which is frequent on parts of the unreclaimed shores, to that of the "artificial marsh-meadow" of Warming (**4**), which affords excellent grazing material for cattle and horses and an abundant yield of coarse hay.

Little Island is about three miles long by about one to one-and-a-half wide, and rises to some hundred feet towards the centre. The rock, which emerges in many places towards the south side, is a magnesian limestone. The whole is well planted with trees and the land is remarkably fertile.

I. Chloride-content and Vegetation.

A slight attempt has been made to correlate the percentage of chlorides, estimated as sodium chloride, with the type of vegetation. Sir E. J. Russell (**2**) cites experiments which show that a slight amount of chloride is in some cases beneficial, but "beyond a relatively low concentration limit further increases in amount of sodium chloride proved toxic." Sodium does not appear to be essential even to salt-marsh plants, but A. C. Halket (**1**) found that *Salicornia* grew better in its presence.

The method employed for chloride estimation is that given by H. J. Page (**3**) of Rothamsted, where the extract from a known weight of soil is treated with a known volume of standard silver nitrate and the excess titrated with decinormal ammonium thiocyanate, using ferric sulphate as indicator.

The first sample of soil was taken outside the sea wall from a part of the beach flooded at high water; the remaining samples were taken inside the sea wall from parts of the reclaimed marsh at varying levels above the drainage water.

Percentage of sodium chloride in soil	Flora of Region	Frequency
7·36	Statice Limonium Spergularia rubra Festuca rubra	Abundant
2·31	Triglochin maritimum Juncus obtusiflorus	Very abundant
	Agrostis alba	Abundant
	Carex vulpina Apium graveolens Aster tripolium	Frequent
2·09	Agrostis alba	Very abundant
	Juncus glaucus Cirsium arvense	Abundant
	Trifolium repens Potentilla anserina Carex vulpina Festuca rubra	Frequent

Percentage of sodium chloride in soil	Flora of Region	Frequency
0·28	Ranunculus repens	Very abundant
	Leontodon hispidus	Abundant
	Juncus communis J. obtusiflorus Holcus lanatus	Frequent
	Cynosurus cristatus Agrostis alba Lotus corniculatus Alopecurus pratensis	Occasional
0·23	Agrostis alba	Very abundant
	Mentha arvensis Ranunculus repens Trifolium repens	Frequent
	Cirsium arvense Festuca rubra	Occasional

II. Transition Vegetation (Reclaimed).

The reclaimed land marked *A* on the map (Fig. 1) contains a long drain from the higher reclaimed land *C*, and a somewhat large pool near its centre. This marsh is cut off from the sea by a long wall, banked up on the inner side

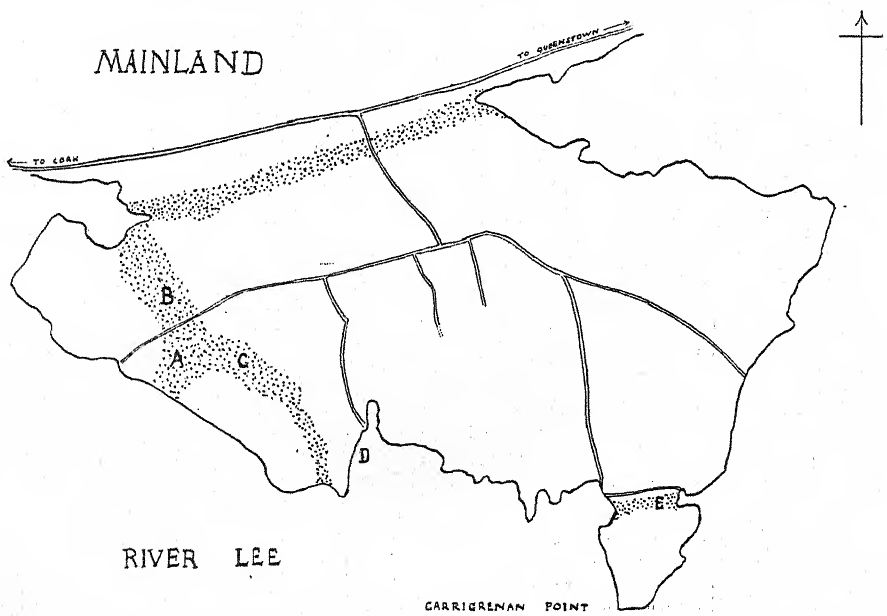


Fig. 1.

by dredgings from the river-channel, and it appears to be customary to run off the drainage-water once yearly. At high tide the greater part of this land, and also that marked *B*, is much below the level of the river outside. These two tracts which were originally one are now separated by an embanked road, and on the whole *B* is drier than *A*.

The method employed for tabulating this vegetation was to take quadrats in typical patches at regular distances apart with the view of noting the influence of increasing dryness of the soil on the flora.

	Quadrats in *A*		Quadrats in *B*
Wettest region.			
%		%	
40	Triglochin maritimum	40	Juncus glaucus
40	Juncus obtusiflorus	20	Potentilla anserina
10	Agrostis alba	10	Trifolium repens
5	Carex vulpina	10	Lotus corniculatus
5	Apium graveolens Aster tripolium	5	Holcus lanatus
		5	Ranunculus repens
		10	Moss Trifolium pratense Epilobium palustre Arenaria uliginosa Geranium dissectum Carex vulpina
Drier region.			
65	Agrostis alba	30	Holcus lanatus
15	Triglochin palustre	20	Ranunculus repens
15	Potentilla anserina	10	Juncus glaucus
5	P. erecta	10	Agrostis alba
		10	Moss
		10	Juncus bufonius
		10	Prunella vulgaris Carex axillaris Lotus corniculatus Potentilla tormentilla P. anserina Rumex nemorosus
Drier still.			
30	Agrostis alba	30	Ranunculus repens
15	Trifolium repens	20	Agrostis alba
15	Juncus glaucus	15	Rumex nemorosus
15	Cirsium arvense	15	Cirsium arvense
10	Carex axillaris	5	Juncus glaucus
10	Festuca rubra	5	Trifolium pratense
5	Ranunculus repens Vicia sepium	5	Holcus lanatus
		5	Prunella vulgaris
		5	Rumex acetosa Plantago major Potentilla anserina Lotus corniculatus
Driest region.			
60	Agrostis alba	70	Agrostis alba
15	Mentha arvensis	15	Rubus fruticosus
10	Ranunculus repens	5	Cirsium arvense
10	Trifolium repens	10	Urtica dioica Rumex sanguineus (?) Ranunculus repens Geranium robertianum Prunella vulgaris Galium aparine
5	Cirsium arvense Festuca rubra		

The greater variety in the flora of the drier land *B* over that of the wetter *A* is fairly well marked.

The reclaimed lands joining the "island" to the mainland have, perhaps, a special interest, as some of them at any rate are in a more advanced state of reclamation than the foregoing. For purposes of comparison the approximate composition of the vegetation on the high ground immediately facing the mainland is given.

High grassland opposite mainland

Trifolium repens Holcus lanatus Dactylis glomerata Alopecurus pratense Cynosurus cristatus	Very abundant
Cirsium arvense	Abundant
Plantago media Trifolium pratense	Frequent
Campanula rotundifolia Ranunculus acris	Occasional
Prunella vulgaris Rumex nemorosus Achillea millefolium Centaurea nigra	Rare

Dry reclaimed marsh near mainland

Agrostis alba Holcus lanatus	Very abundant
Trifolium repens Ranunculus repens	Abundant
Plantago major Rumex nemorosus Ranunculus acris Potentilla anserina	Frequent
Juncus communis	Occasional
Bellis perennis	Rare

Wet reclaimed marsh near mainland

Juncus communis	Very abundant
Agrostis alba Potentilla anserina	Abundant
Holcus lanatus	Frequent
Ranunculus acris Lotus corniculatus Rumex nemorosus Trifolium repens	Occasional

III. TRANSITION VEGETATION (UNRECLAIMED).

The inlet marked *D* on the map displays a natural salt-marsh vegetation. A typical piece is represented by the following:

20 %	*Statice Limonium*	5 %	*Samolus Valerandi*
20 %	*Festuca rubra*	5 %	*Suaeda maritima*
10 %	*Salicornia herbacea*	30 %	Rocks
10 %	*Aster Tripolium*		

A line transect from the river (or sea) side of this to the beginning of cultivation yielded the following sequence of plants:

SEA END
Salicornia herbacea
Spergularia sp.
Statice limonium
Suaeda maritima
Salicornia herbacea
Spergularia sp.
Suaeda maritima
Samolus valerandi
Festuca rubra
Statice limonium
Samolus valerandi
Armeria vulgaris
Aster tripolium
Plantago maritima
Chenopodium rubrum
Suaeda maritima
Spergularia sp.
Spergularia sp.
Beta maritima
Agropyrum caninum
Beta maritima
Sonchus arvensis
BEGINNING OF CULTIVATION

What appears to the writer to be a particularly interesting comparison is afforded by the two following transects taken just outside and just inside the sea-wall of the marsh marked *E* on the map.

Outside Sea Wall	Inside Sea Wall
Green Alga [Rhizoclonium?]	Salicornia herbacea
Salicornia herbacea	Plantago maritima
Festuca rubra	Glyceria maritima
Samolus valerandi	Samolus valerandi
Aster tripolium	Spergularia sp.
Festuca rubra	Glaux maritima
Salicornia herbacea	Glaux maritima
Spergularia sp.	Festuca rubra
Statice limonium	Trifolium repens
Festuca rubra	Carex vulpina
Plantago maritima	Luzula campestris
Suaeda maritima	Festuca rubra
Statice limonium	Potentilla anserina
Festuca rubra	Lotus corniculatus
Chenopodium rubrum	Centaurea nigra
Aster tripolium	Festuca rubra
Statice limonium	Trifolium pratense
Festuca rubra	Leontodon hispidus
Beta maritima	Ranunculus acris
Poa annua	Juncus communis
Potentilla anserina	Festuca rubra
Matricaria inodora	Carex vulpina
Rumex nemorosus	Bellis perennis
Festuca rubra	Cynosurus cristatus
Plantago coronopus	Holcus lanatus
	Ranunculus repens
	Cirsium arvense
	Spiranthes autumnalis

As far as could be ascertained Tansley's view (**3**, p. 68) appears to be borne out that "there is no good evidence that salt marsh can develop by the mere accumulation of silt or humus, without human assistance, into a non-maritime vegetation."

In conclusion I wish to thank Mr E. Standish O'Grady, of Little Island, for his very kind permission to move freely about his property; Mr P. Tate, of the Botany Department, University College, Cork, for his very courteous help in the identifications of some grasses; Mr Michael Twohig for placing his topographical knowledge of the locality so freely at my disposal; and my son Andrew, without whose untiring help the work could not have been accomplished. I have received the kindest help from Prof. H. A. Cummins and Mr J. O. Jagoe, of the Botany Department, University College, Cork, in the re-identification, which was thought desirable, of a few of the species included in the lists.

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(3) **Tansley, A. G.** *Practical Plant Ecology*, 215, 68. London, 1923.
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NOTICES OF PUBLICATIONS OF GENERAL BEARING

THE PLANT AS AN ECOLOGICAL INSTRUMENT.

(1) **Clements, F. E.** and **Weaver, J. E.** "Experimental Vegetation." *Carnegie Instit. Washington Publ.* **355**, 1924.

(2) **Clements, F. E.** and **Goldsmith, G. W.** "The Phytometer Method in Ecology." *Ibid.* **356**, 1924.

These two papers, from slightly different aspects, embody the results of an attempt to use plants, or plant communities, as the best measures of reaction to the habitat, in ecological studies. While the value of methods based on this ideal will be obvious, it is equally clear that considerable work is required before suitable methods are evolved, and we may hope that these are to be only the first of a series of papers dealing with this subject. In the first paper, the subject of study is the North American grasslands, the object being to estimate the relative importance of the various vegetation units and their inter-relationships. The methods employed are: (1) sowing seeds, (2) planting seeds or propagules, (3) planting seedlings, (4) transplanting adult plants of various ages, (5) transplanting small communities or portions of communities. In short, these methods aim at observing migration and the subsequent development of vegetation, but under controlled conditions. Accessory to these basic methods are the use or modification of the various factors which may play on the developing plants or vegetation, particularly competition, destruction by animals and the various physical factors. Along with these are checks by instruments and phytometers of the habitat factors. Various methods of altering the physical factors or reducing or modifying competition are employed, of which the simplest and most satisfactory prove to be: (1) sowing on the surface in the midst of natural vegetation; (2) sowing or planting in trenches, by which competition is prevented for a short time; (3) sowing or planting in denuded areas, which eliminates competition for a much longer period, but which makes the water relations less favourable while improving the light relations; (4) transplanting adult plants, either into living cover or into denuded areas; (5) improving the conditions for germination and establishment, by watering, shading, draining or thinning.

The material used included a great variety of grasses, "forbs" (herbs other than grasses), shrubs and trees. These were germinated or transplanted at four climatic stations, representing typical conditions in each of the four main grassland communities between the Missouri River and the Rocky Mountains. A number of edaphic stations represented the various edaphic conditions at each of the climatic stations. It is impossible to summarise adequately the enormous amount of material provided by these experiments, but the results indicate quite clearly that germination and growth of practically all species are reduced as the climatic conditions become drier (i.e. going westwards in the prairie region). The authors therefore regard rainfall and holard as all important, the other factors in plant growth being secondary. On the other hand the luxuriant vegetation in low prairie—associated with more humid conditions—had a decided effect in reducing the establishment of introduced plants, largely through the reduction in light intensity with which the seedlings

had to contend. The possibility of tree growth under natural conditions on stabilised grasslands appears to be almost nil, since the seedlings are shaded out in the lowlands and destroyed by drought in the uplands.

In the second paper, by Clements and Goldsmith, attention is directed more towards the examination of the effects of the various physical factors by means of *phytometers*, that is, cultures of similar plants of one species in the different habitats considered. The methods employed are described in detail, the plants used being chiefly sunflower and wheat, grown in containers which were sealed to allow of measurements of water loss. The principal comparison made is that between the growth of the phytometer plants at three stations near Pike's Peak, Colorado, designated *plains*, *montane* and *sub-alpine* stations, the natural vegetation of the three main stations being mixed prairie, mixed coniferous forest, and spruce forest respectively. The transpiration per square decimetre of leaf area was highest on the plains and lowest at the sub-alpine station, but the montane station was generally the most favourable for leaf area and stem diameter. Stem length of sunflowers, however, was greatest on the plains. Similarly, there is much variation in the weight of plant produced. Generally, however, sunflowers and beans made best growth on the plains, while wheat and oats did best at the montane station. The water requirement, namely, the amount of water used in the production of 1 gm. of dry material, as defined by Briggs and Shantz, normally decreases with the increase in the altitude at which the plants are grown. A further comparison between the dry warm (*xerocline*) side of a canyon, and its cool moist side (*mesocline*), showed that the former, in its effect on sunflower growth, resembled the plains region—while the mesocline presented typical montane conditions. These results make it clear why the south slope is covered with scrub and grassland dominants of the plains while the north slope is dominated by characteristic montane forest.

Some interesting general conclusions are worthy of notice. Transpiration does not appear to vary consistently with any single instrumental record. No better correlation exists between transpiration and evaporation from a white cylindrical atmometer cup than between transpiration and average temperature. This is to be expected when the composite nature of the factors affecting water loss from a plant is considered, and it is a conclusion which seems to justify the statement that when phytometers are used they are, or may be, a sufficient measure of the factor-complex and render recording instruments unnecessary except in the most elaborate installations. This would seem to be particularly true when the water relations of plants are under consideration—and phytometers such as those employed by Clements and Goldsmith are clearly much more adequate than the rather unsatisfactory atmometers at present in use. The experience of the reviewer suggests that an additional measurement might profitably be made when the phytometer plants have grown for a whole season and their water relations are being estimated. This measurement is the water content of the plant, perhaps most readily expressed by dividing the fresh weight by the dry weight. A brief reference is made in the text to one case in which this ratio varied but the data are not given in the tables.

One fact emerges very clearly from a study of the data—that growth, as measured by increased dry weight, usually shows very little relation to the water loss or water requirement. The authors show that sunflowers and beans normally grow best at the *plains* station, while wheat and oats are most successful at their *montane* station, and they suggest that the former plants have a higher temperature optimum. An analysis of this temperature effect would have proved of great interest, for on the present evidence it seems to be of far greater importance than transpiration alone—which varied in the same way at the different stations whatever the species of plant used. The apparent lack of connection

between transpiration and growth in these observations certainly demonstrates the need for standardised plants for phytometer work. A complete study of a suitable standard species grown under a wide range of environmental conditions is required before the phytometer can rank as an instrument of precision. The value of the method as an aid to the study of vegetation is, however, amply demonstrated by the papers under consideration.

W. H. PEARSALL.

SAP DENSITY AND WATER SUPPLY.

Korstian, C. F. "Density of Cell Sap in relation to Environmental Conditions in the Wasatch Mountains, Utah." *Journ. Agric. Res.* **28**, pp. 845–907. 1924.

This is an investigation undertaken with the object of gaining further insight into the relations of plants to the conditions of the environment, especially in regard to forestry and forest regeneration. In this problem the water relations take a very prominent place, and an investigation of the osmotic forces of the cell sap was considered as affording useful information. The work was carried on in the Wasatch Mountains in Utah, and the area covered extends from Sage Brush on the one hand, to the montane tree limit on the other, at altitudes varying from 5000 to 11,500 feet, and covering a great variety of physiographic features. The material tested was collected in sealed tubes and the sap extracted by the freezing method. A special convex cup and concave presser were used. Care was taken to avoid water loss after collection. Data are given of the environmental conditions of the chief habitats studied, especial attention being paid to temperature, soil moisture, and evaporation.

A considerable number of plants were investigated; in most cases samples of each species being collected from more than one locality. The table of the results of determinations of the osmotic power of the cell sap occupies 23 pages. In the discussion of the results emphasis is laid on the correlation between sap density and water supply. The density is lower in the roots where these have been tested. The value obtained for any plant is not a constant. There is a daily fluctuation, a rise in the forenoon and a fall towards evening. Sun plants gave higher values than those in shade. A close relation seems to exist between photosynthesis and sap density. Large plants, trees, etc., always gave higher values than herbaceous species. In a tree there is an apparent osmotic gradient, the lower leaves having lower values than those higher up.

A seasonal fluctuation of density was also demonstrated. Young leaves have a uniformly lower value than old ones. Otherwise the seasonal variation follows the habitat conditions: the maximum density occurs in the dry part of the summer. In winter a variable state of things was found. Conifers had low values while evergreen shrubs had high ones. This difference is apparently directly correlated with the nature of the food reserves; in conifers in winter fats and oils appear in quantity in the leaves, while in evergreens starch was converted to sugar.

Individual species showed great variation in value according to the habitat. Average results of all the plants tested in each habitat gave results which accord very closely with the degree of xerophily of the habitat. Averages of the plants from successional stages showed a progressive decrease in density as the succession advances. The density showed

some relation to structural features; those plants with structural features tending to a reduction of transpiration, or with water-storage tissue, had uniformly low figures. The parasites studied had higher values than their host plants.

Capacity to resist injury from drought, frost or other factors bore a close relation to the osmotic power of the cell sap. The higher the value the hardier was the plant.

R. S. A.

MEASUREMENT OF WATER LOSS.

Weaver, J. E. and **Crist, J. W.** "Direct Measurement of Water Loss from Vegetation without disturbing the Normal Structure of the Soil." *Ecology*, **5**, 2, pp. 153–170. 1924. Pl. III.

The objection to the ordinary method of determining water loss is that the plant is growing in a disturbed soil that is very different from that of the field. Further, unless any large containers are used the root systems are seriously cramped. A method has been devised for measuring the water loss without disturbing the soil. Metal cylinders of one square foot cross sectional areas are used to cut out an area of vegetation and then iron cylinders of three foot length are forced tightly over the column of soil. This is then excavated, the lower end sealed up, and the whole sunk in a suitable trench. The containers are weighed before being put in the trench and at the end of the experiment. In this way samples of undisturbed natural vegetation or of crops can be studied.

Experiments were carried out with these methods on the short grass plains, on mixed prairie, and on prairie vegetation. During the experiments the containers with their columns of soil were protected from rainfall. Water was added carefully and slowly so as to give an even distribution through the soil. Direct loss of water from the soil and from soil covered by dead plants was determined. Crop plants were found to give off more water than the native vegetation. The latter gave off sufficient in the period of the experiment to furnish the mean precipitation. The advantages of the method for the study of the problems of the relations of the plant to soil and soil moisture are very great as these can be tackled with natural conditions for the absorbing organs.

R. S. A.

ANIMAL ECOLOGY.

Alkins, W. E. "The distribution of Pisidia in the Oakamoor district of the Churnet Valley." *Trans. North Staffs. Field Club*, 1924–25.

With the help of A. W. Stilfox the author has made a detailed study of the ecological relations of the eight species of these small bivalve mollusca which occur in a restricted area in North Staffordshire. The habitats include parts of a disused canal, streams, ditches, ponds and a marsh, and the transition is traced from the river-canal association of *P. subtruncatum*, *nitidum*, *henslowanum* and *milium* to the ditch-marsh society of *P. casertanum* and *personatum*.

A. E. B.

NOTICES OF PUBLICATIONS ON BRITISH VEGETATION

A BRITISH WOODLAND NEAR LONDON.

Marriott, St John. *British Woodlands as illustrated by Lessness Abbey Woods.* London: Routledge and Woolwich Pioneer Press, 1925. Pp. xviii + 72, with photographic plates of scenery and a sketch map.

This is a very interesting and praiseworthy little booklet, inspired by the "Regional Survey" movement through the agency largely of Mr C. H. Grinling, and promoted by various local scientific societies. There is a historical, topographical and geological introduction by Mr Grinling, and the body of the work consists of Part I, including a vegetational survey (illustrated by the sketch map), a complete list of plants comprising *all* the terrestrial groups of the plant kingdom, and Part II, including lists of mammals, birds, reptiles, amphibia, fishes, galls, lepidoptera, molluscs and fossils.

Mr Marriott is a keen field naturalist and he has invoked the aid of many specialists, so that the determinations of species may be taken as really trustworthy. His vegetation survey (illustrated by charts of special localities) brings out very clearly the effect of the various soils on the flora and vegetation. To the ordinary seasonal "aspects" of vegetation, Mr Marriott happily adds a "hiemal" aspect. The wood is evidently semi-natural, though there has been a fair amount of planting and some other disturbances of the natural relationships of the vegetation.

It is much to be desired that other local societies should follow this excellent example, especially where areas of natural and seminatural vegetation still exist in the neighbourhood of large towns and cities, before it is too late. Such accounts provide indispensable data for the student of vegetation and of ecology and natural history in general, as well as stimulating local pride in natural areas of country near great centres of population, areas which are not yet spoiled or destroyed and which in some cases may still be saved.

A. G. T.

A SCOTTISH AREA.

Patton, Donald. "The Vegetation of the Tinto Hills." *Ann. of the Andersonian Naturalists Society*, **4**, 2. Glasgow, 1925. Pp. 30–51.

The Tinto Hills in Upper Clydesdale, Lanarkshire, belong to the Southern Uplands of Scotland. Tinto itself reaches a height of 2335 feet, the other summits ranging from 1472 to 1925 feet. The annual rainfall exceeds 45 inches in places, and mist is very prevalent. The mean January temperature is about 35° F.; July, 57° F. The whole region, including the summits, was glaciated and there is a thick layer of Boulder Clay round the bases of the hills. The Clyde has cut this away and formed a rich alluvial tract. The hills themselves are felsite.

The author divides the region into a lowland division, including (1) Aquatic, (2) Gravel, (3) Alluvium, (4) Boulder Clay, and a hill division, including *Calluna-Pteridium*, *Calluna-Erica cinerea* and *Calluna-Vaccinium* zones. The lowland zone has been much altered by farming. The Boulder Clay has been extensively limed, and there are many introduced plants. The heavier clay at higher altitudes has also been limed and bears good pasture of native grasses and sedges. The whole of the hill division may be regarded as a *Calluna* heath, this species extending to the summits, though much less abundant than at lower levels. In the *Calluna-Vaccinium* zone *V. myrtillus* gives place upwards to *V. vitis idaea*, and there is an abundance of lichens and mosses.

The paper concludes with a tabular list of the flora arranged under the zones given, to which is added some account of "Railway vegetation."

A. G. T.

NOTICES OF PUBLICATIONS ON FOREIGN VEGETATION

FINNISH FORESTS.

(1) **Cajander, A. K.** "Ueber Waldtypen." 1909. *Acta forestalia fennica,* **1.**

(2) **Cajander, A. K.** "(*a*) Über die Verteilung des fruchtbaren Bodens im Finnland und über den Einfluss dieser Verteilung auf die wirtschaftlichen Verhältnisse im Lande. (*b*) Was wird mit den Waldtypen bezweckt?" 1923. *Ibid.* **25.**

(3) **Cajander, A. K.** and **Ilvessalo, Y.** "Ueber Waldtypen II." 1921. *Ibid.* **20.**

(4) **Ilvessalo, Y.** "Vegetationsstatistische Untersuchungen über die Waldtypen." 1922. *Ibid.* **20.**

(5) **Ilvessalo, Y.** "Ein Beitrag zur Frage der Korrelation zwischen den Eigenschaften des Bodens und dem Zuwachs des Waldbestandes." 1923. *Ibid.* **25.**

(6) **Ilvessalo, Y.** "The Forests of Finland." 1924. *Communicationes ex Instit. Quaest. Forest. Finland.* Editae **9.**

The results of the Finnish Forest Survey appear to have reached a stage at which a general outline of Finnish woodland ecology can be obtained. The survey deals with the results of estimations of the forest vegetation, tree production and soil character, along thirty-nine survey lines, twenty-six kilometres apart and running south-west to north-east over the whole of Finland. On the data obtained from these survey lines, a very complete description of the forest resources of the country is possible. The degree to which the country is still covered by its native vegetation may be gauged from the fact that 73 per cent. of the area is still forest, and about 15 per cent. is waste land, chiefly *Sphagnum* bog (7 per cent.) and "pine swamp" (4 per cent.). The composition of the forest naturally varies very considerably with the variations in soil and climate. Pine (55) and spruce (25) dominate 80 per cent. of the forest land, the remainder being chiefly birch forest (17 per cent.), although alder and aspen may also be dominant in the south. Birch is more prevalent in the north owing to its ability to grow in the barren *fjeld* regions.

The distribution of the trees is otherwise largely determined by the nature of the soil, and a number of ground flora types are recognised, each of which usually occurs on a characteristic type of soil. Excluding local modifications, the chief forest types are:

1. *Sanicula* type (ST). With numerous herbaceous species like *Paris quadrifolia*, *Milium effusum* and *Majanthemum bifolium.* Occurs on calcareous soils in the south-west.

2. *Oxalis-Majanthemum* type (OMaT). Smaller thin-leaved species more abundant. On fertile soils in the south.

3. Fern type (FT). In valleys on soils like 2.

4. *Oxalis-Myrtillus* type (OMT). On clayey or damp soils.

5. *Myrtillus* type (MT). With an almost continuous covering of mosses, chiefly *Hylocomium* spp. Found on only moderately fertile soils of morainic origin.

6. *Vaccinium* type (VT). *V. vitis-idaea* and *Hypnum parietinum* most abundant. Very widespread on morainic matter.

7. *Empetrum-Myrtillus* type (EMT). Common in the north.

8. *Calluna* type (CT). On the drier and coarser morainic soils.
9. *Cladina* type (ClT). Dry sandy soils in the north.

While there is no hard and fast relation between these types and the tree dominants, nevertheless pine is the normal dominant along with the heathy types of ground flora 6–8. Spruce is the typical dominant when the forest type is 4 or 5, although pine covers considerable areas, about one quarter, of these soils also. The soils occupied by forest types 1–3 are covered by the small areas of deciduous forest, and in these pine is normally absent. Much of the deciduous forest seems, however, to be of secondary origin. Forest destroyed by fire and deserted clearings are normally colonised by birch, aspen or *Alnus incana.* Alder woods are almost restricted to the damper lands which have been burned over for agricultural purposes.

The *Vaccinium* type, with pine dominant and spruce frequent, is probably the most widely spread type of forest, although the *Myrtillus* type is more important from the point of view of timber yield, as it is nearly as widespread and is much more productive. The relative areas, timber yields and soil types are most conveniently summarised in the following table, amplified from Cajander (2). The figures for lime and total nitrogen are relative, the detailed figures being given by Ilvessalo (4), who shows that the lime and total nitrogen—of the various soil factors—possess the highest degree of correlation with the timber production.

Forest type	Distribution as per cent. of forest area		Soil type (upper 20 cm.)		Annual increase of normal		No. of species of Phanerogams
	North	South	Lime (CaO)	Total N	Pine stands	Birch stands	
2. OMaT	1	6	140	223	—	185	158
4. OMT			117	137	115	117	119
5. MT	4	38	100	100	100	100	100
6. VT	18	31	79	71	83	83	73
7. EMT	26	—	—	—	(32)	—	—
8. CT	10	7	54	64	52	—	41
9. ClT	9	—	36	34	27	—	20

The correlation between the lime content of the soil, the timber yield and the relative number of flowering plants as revealed in this summary is very striking, and it suggests a high degree of dependence of the plant covering upon the lime content of the soil.

W. H. P.

CORAL REEFS OF CUBA.

Uphof, J. C. Th. "The Plant Formations on the Coral Reefs along the Northern Coast of Cuba." *Amer. Journ. Bot.* **11**, pp. 409–416, 1924.

The reefs form masses of stone near the shore or at some distance out. In height they vary from 30 metres down to about 2 metres or less above the sea. From sea-level to a height of 3–5 metres constant washing by sea water occurs. The plants are not only halophytic but able to endure a very calcareous substratum. The Algal flora is briefly mentioned, but this has not been fully worked out. Of low plants, those that grow nearest the sea water are typical halophytes with more or less succulent leaves or stems, *Sesuvium microphyllum*, *Phylloxerus*, and *Salicornia*, with *Distichlis spicata*. Other species predominate on higher reefs, e.g. *Conocarpus erecta*, which is very stunted near the shore, but almost a tree when protected. At a distance of 20–30 metres, where sand has collected on the reef, a much more luxuriant and varied vegetation occurs, consisting of plants without marked halophytic features.

R. S. A.

VEGETATION OF THE ARID PORTIONS OF NORTH AMERICA.

Shantz, H. L. and **Piemeisel, R. L.** "Indicator Significance of the Natural Vegetation of the South-Western Desert Region." *Journ. Agric. Res.* **28**, p. 721, 1924.

The region considered is in southern California and Arizona with part of Nevada and Utah. The whole area is arid, having a rainfall of from 2–7 inches in the valleys, though rising to 15 inches on the upper lands. Two areas are considered in some detail, one in California, the other in Arizona, and the plant communities correlated with the physical factors. Then the communities are considered in their wider aspect and the general range of factors controlling each is given. The chief communities are:

1. *Yucca* and *Cactus* Association, which occurs on hill slopes. This is replaced by Giant Cactus and Paloverde (*Cercidium torreyanum*) in Arizona.

2. Creosote Bush (*Covillea glutinosa*) Association, which is the most widespread. This occurs on light soils of about 4 ft. depth, which are permeable and well drained and which become very dry in summer. The soil is not saline.

3. Desert Sage (*Atriplex polycarpa*) Association. This occurs at lower levels with higher temperature. The soil is finer and has a greater moisture-holding capacity than that of the creosote bush association. The soil is generally liable to floods in winter, but is very dry in summer. The available water is less than in the former association; the salt content is higher but small.

4. Mesquite (*Prosopis glandulosa*) Thicket. This occupies the bottoms of valleys. The soil is like that of the desert sage association but has a higher water table so that available water is always present in the first 4 ft. of soil. Salinity is higher.

5. Narrow-leaf Saltbush (*Atriplex linearis*) Association. This occupies low flat depressions with a heavy compact soil which becomes very dry in summer. The salt content is higher, especially in the deeper layers. This community indicates a much shallower soil than desert sage.

6. Salt Grass (*Distichlis spicata*) Association. This is of limited extent. It occurs in very saline soil with a high water table.

7. Washington Palms (*Washingtonia filifera*) occur as scattered groups or communities round springs or streams.

8. Pickleweed (*Allenrolfia occidentalis*) Association occurs at the bottoms of valleys where an excess of salt is present in the surface layers of soil.

9. Mesquite (*Prosopis glandulosa*) and Chamiso (*Atriplex canescens*) is an association characteristic of sandhills.

10. Arrowweed (*Pluchia sericea*) and Saltbush (*Atriplex lentiformis*) Association is a community of local occurrence. It is present in soil like that of the pickleweed association, but with a coarse subsoil and a lower salt content below the surface.

11. Seepweed (*Dondia* spp.) Association occurs in level valley bottom with a high water table and a high salt content.

12. Bare flats occur scattered through the lower parts of the valley. The soil is heavy and the water stands on the surface after rains, but in dry weather cracks freely. The salt content is very high. These flats are either devoid of plants or have a very scattered vegetation in the most favourable places near the edges.

Each of these associations is described, the botanical features given, and a full statement of the chief physical factors. The description of the communities is followed by a discussion of the relations to climatic factors and especially to rainfall and temperature. A correlation is also made between the natural vegetation and the character and productiveness of the

land. In this connection it is pointed out that the various associations have a wide range of conditions, so that it is necessary to know more than the vegetation type before any interpretation of the potentialities of the soil can be made. Some details of the association must be given; in fact if a primary ecological survey is made, a fairly accurate measure of land values is reached.

Throughout the paper there are full tables of soil analyses, water contents and physical and climatic factors. The paper is illustrated by ten plates, each containing two photographs of high quality.

R. S. A.

Aldous, A. E. and **Shantz, H. L.** "Types of Vegetation in the Semiarid Portion of the United States, and their Economic Significance." *Journ. Agric. Res.* **28**, pp. 99–128, 1924.

The principal vegetation types occurring west of the hundredth meridian are enumerated, and their distribution and conditions briefly indicated Notes are also given of the possibilities for crop production, either of grain or forage plants, and for grazing. Altogether 102 vegetation types are enumerated. These types are then grouped according to their possibilities for dry farming, for grain production, and for forage plants. A tabular key of the carrying capacity for stock is given; and the geographical distribution according to regions which cover practically the whole range. There are 32 photographs on 16 plates in illustration. The paper, though merely an outline scheme, is valuable in showing the uses of ecology for practical purposes and suggests lines that might well be adopted in other countries, where the agricultural community is advancing to untouched regions. A preliminary ecological survey and land classification of this kind would certainly result in fewer failures and ultimately in much greater economy of production.

R. S. A.

VEGETATION OF ARID AUSTRALIA.

(1) **Osborn, T. G. B.** and **Wood, J. G.** "On the Zonation of the Vegetation in the Port Wakefield District, with special Reference to the Salinity of the Soil." *Trans. Roy. Soc. South Aust.* **47**, 244, 1923.

(2) **Osborn, T. G. B.** and **Wood, J. G.** "On some Halophytic and Non-halophytic Communities in Arid South Australia." *Ibid.* 388, 1923.

(3) **Wood, J. G.** "On Transpiration in the Field of some Plants from the Arid Portions of South Australia, with Notes on their Physiological Anatomy." *Ibid.* 259, 1923.

These three papers form part of what promises to be a detailed investigation of the vegetation of the arid portions of South Australia. A very large proportion of this region is occupied by an open community of small shrubby plants belonging to the family Chenopodiaceae. There are many species of *Atriplex* (Saltbush) and *Kochia* (Bluebush)[1]. These communities, though of such wide extent, have either been neglected by plant geographers or treated as communities of Halophytes. This view is based on the systematic position of the plants, the Chenopodiaceae containing a large number of halophytes, and on the low lying nature of the country they inhabit and the fact that in most cases the bottom water is decidedly salt. The present papers mark the commencement of a detailed study of these communities.

1. In the first a study is made of the zonation of communities passing from those under the influence of sea water at the coast up to Saltbush communities further inland. Excluding the Mangroves, which are treated as belonging to a separate formation, a view that need not be considered at the moment, four communities are recognised and briefly

[1] "Saltbush" is a general name applied to various low shrubby species of *Atriplex, Rhagodia* and *Kochia*, "Bluebush" to white tomentose species of *Kochia*, e.g. *K. sedifolia*.

described. The characteristic plants of these are *Arthrocnemum arbuscula*, *A. halocnemoides*, *Atriplex paludosum* and *A. stipitatum*. These communities show a decreasing water content of the soil and a decreasing salt content, both of total salts and of sodium chloride. The figures of the saltbush communities are so small for salts, 0·3–2·8 per cent., that they cannot be regarded as truly halophytic.

2. This paper deals with some of the communities of these Chenopodiaceous plants in the inland portions; communities of Saltbush (*Atriplex vesicarium*), Mallee (*Eucalyptus oleosa*) with Saltbush, *Kochia planifolia* and Bluebush, *Kochia sedifolia*, are described and analyses of the soils of each given. The soils are all exceedingly dry, 2–8 per cent., with a low salt content, 0·1 to 0·18 per cent. total salts of which 0·3 to 0·6 per cent. is NaCl. The reaction is slightly on the alkaline side of neutral (*p*H 7·4 to 7·7). By contrast with these, communities in two salt lakes are described; the first is a gypsum lake where *Arthrocnemum halocnemoides* var. *pergranulatum* is the chief plant. The soil here has 4·97 per cent. of soluble salts of which 0·68 per cent. is NaCl. The reaction is more alkaline, *p*H 8·2. This community gradually merges into the saltbush and intermediate soil conditions are found. In another lake where the soil contained 6·6 per cent. of soluble salts with 3·52 of NaCl, *Pachycornia tenuis* formed a pure community. These last two, which are decidedly halophytic, are sharply marked off from the others both in habitat and soil and also in general facies. The shrubby species of *Atriplex* and *Kochia* are considered as forming the typical flora of arid regions in South Australia and are compared to the Karroo flora of South Africa.

3. This paper deals with the physiological anatomy of some of the plants in these communities and also with the transpiration under field conditions. Transpiration was measured by means of burette potometers according to Lloyd's method. Of the plants examined, three types of transpiration curve are noted: (*a*) *Casuarina lepidophloia*, which has a relatively high rate and a curve which follows closely that of evaporation. (*b*) *Geijera parviflora* and *Pholidia scoparia*, which have a low transpiration rate. While the maxima correspond to the maxima for evaporation there is not close agreement for minor fluctuations. (*c*) The third group contains the shrubby Chenopodiaceae *Kochia sedifolia*, *Atriplex vesicarium* and *Rhagodia gaudichaudiana*. The transpiration curves in these are all very similar. The rate is practically constant at a low figure during the day with a fall at night which takes place later with *Kochia* than the others. These Chenopodiaceous plants have a dense covering of hairs, vesicular in *Atriplex* and *Rhagodia*; *Kochia* has a thick felt of hairs which probably functions for water absorption. R. S. A.

Wood, J. G. "The Relations between Distribution, Structure and Transpiration of Arid South Australian Plants." *Trans. Roy. Soc. South Australia*, **48**, pp. 226–235, 1924.

This paper is a continuation of the author's work on the water relations of plants in South Australia. The present account deals with experiments carried out on the central plain of Australia at Curnamona, which is some miles south of Lake Frome. The rainfall here is about seven inches, but very uncertain. Six species are studied, three being plants which are "character" species of the plains, two are plants from watercourses and the last is a parasite (*Loranthus quandang*). An account is given of the anatomy of the leaves. These plants show very different transpiration rates; the plains species have a much lower rate, especially so in the case of the Saltbush, *Kochia planifolia*, which gives an almost flat curve for a 24-hour period. *Kochia* is here the most prominent plant and appears the best suited to the conditions. In addition to its other features the leaves have a thick covering of hairs. The stream bed plants show a higher rate, one, a shrubby Acacia (*A. victoriae*), only slightly so, but the other, *Senecio magnificus*, a herbaceous plant, shows a very uneconomical usage of water. Especially interesting is the parasite *Loranthus*, which has a much more rapid transpiration rate than its host plant. R. S. A.

NEW SOUTH WALES.

Brough, P., McLuckie, J. and **Petrie, A. H. K.** "An Ecological Study of the Flora of Mount Wilson. Part I. The Vegetation of the Basalt." *Proc. Linn. Soc. of New South Wales*, **49**, pp. 475–498, with Plates LVII–LX and 5 figures in the text. 1924.

With a view to stimulating ecological work in Australia, the Sydney University Botanical Society in 1923 initiated a study of the vegetation of Mount Wilson. The present paper, which embodies some of the results obtained, is largely of the nature of primary survey, which has been carried out for the purpose of studying the relationships and distribution of the various plant communities, and also to lay a foundation for future intensive studies.

After a brief notice on the general features of the Australian flora the authors proceed to discuss the origin of the flora of New South Wales and in particular of Mount Wilson. It is composed chiefly of three elements, an endemic flora consisting largely of *Eucalyptus* forests and occupying the greater part of the state; a Malayan flora finding its chief expression in Rain Forest; an Antarctic flora which occurs as scattered individuals in certain regions. A study of the fossil evidence tends to show that the Malayan flora emanated from the north in the early Tertiary and spread through the greater part of the continent, later being invaded by the endemic flora which originated elsewhere on the continent. Subsequent changes in the physiography of the country resulted in the Malayan flora receding to sheltered habitats controlled by markedly favourable edaphic factors, whilst the endemic flora became adapted to a xerophytic habitat. On Mount Wilson, which is one of a series of residual Tertiary basalt outflows and consists of a sandstone ridge with frequent caps of igneous rock, the Malayan flora occupies the sheltered slopes of the basalt caps and the sandstone gullies, the endemic flora being found on the sandstone plateau. The present paper deals with the vegetation occupying the basalt caps.

Four chief types of vegetation are distinguished: the *Ceratopetalum-Doryphora* Forest; the *Eucalyptus-Doryphora* Forest; the *Eucalyptus-Alsophila* Forest; the *Eucalyptus-Pteridium* Forest. These four, however, are actually variations of two main groups, the *Eucalyptus* Forest on the sandstone and the *Ceratopetalum-Doryphora* Forest on the basalt.

Each of these four types, or "associations" as they are termed, is then discussed in detail. Their habitat, and structure and physiognomy are described and their floristic composition enumerated under their respective strata. In the *Ceratopetalum-Doryphora* association an interesting note is recorded on *Quintinia sieberi*. Young plants of this epiphyte become established among the leaf bases and tangled adventitious roots on the trunks of tree-ferns. Subsequently the roots of the *Quintinia* reach the ground where they become established. This is the only case of hemi-epiphytism encountered in the Rain-Forests at Mount Wilson.

The discussion of the effect of fire on the different types of forest provides some interesting information. Round every junction of these types the vegetation bears "all the indications of having been recently burnt. The fire has crept up to the edge of the basalt, has in places passed through the *Eucalyptus-Alsophila* association, but has never transgressed the humid Rain-Forest." The bush fire is stated seldom to destroy the climax associations, but profound alterations usually occur in the lower layers, often resulting in a pure community of *Pteridium aquilinum*.

Interesting methods of showing the distribution are employed in the text-figures. In the examples of chart and belt transects the idea is to convey a "bird's-eye view" impression. The various components of the vegetation are indicated by symbols but the canopy of the larger components is also outlined, the lower layers showing through or displaying

graphically their denser grouping where not overshadowed by a canopy. In the diagram the approximate ranges and frequency of the basalt flora are depicted in rectangular form, the various types of vegetation being set out along a base line. The range of the dominant through the various types is indicated by a band which is broadest when the dominant occurs most frequently and tapers away in each direction as the dominant loses its position.

T. F. C.

Petrie, A. H. K. "An Ecological Study of the Flora of Mount Wilson. Part II. The Eucalyptus Forests." *Proc. Linn. Soc. of New South Wales*, **50**, pp. 145–166, Plates XX–XXII, and four figures in the text. 1925.

This second part contains an account of some of the salient features of the *Eucalyptus* forests which constitute the vegetation of the sandstone plateau, and supplements the observations recorded in Part I on the *Eucalyptus* communities of the basalt. The main communities in the area under observation are outlined, observations on their distribution and inter-relationships are recorded and some of the more important problems indicated concerning their adaptations, development and other studies awaiting investigation.

In discussing the general physiognomy of the *Eucalyptus* forest it is pointed out that in most cases the association dominants are species of *Eucalyptus* of which there are some three hundred species in Australia. Despite this the physiognomy is characteristically uniform as the species of *Eucalyptus* all present a xerophytic appearance and possess the same growth form. The open nature of their foliage and the comparative isolation of the trees permits a considerable development of the lower layers of the associations.

An interesting comparison is drawn between the *Eucalyptus* forest and the Rain forest previously described; the former is typically xerophilous; the latter, composed of luxuriant vegetation, is typically mesophilous. The interdependence characteristic of the Rain forest is distinctly lacking in the *Eucalyptus* forest, where epiphytes are scarce and ombrophytes absent. The Rain forest at Mount Wilson, on account of the severity of the climate, is, comparatively, of a poor floristic composition.

It is interesting to find that for the classification of the communities the author has adopted Clements' system with Tansley's conception of climax communities, though it is natural that there are instances where he finds it necessary to consider modifications to suit local requirements. For instance, he states that the structure of the *Eucalyptus* forest is likely to be responsible for many problems connected with the definition of status. It is no uncommon occurrence for one society of shrubs to occur in two different associations, and the typical substratum of a *Eucalyptus* association may occur where the development of trees is inhibited. The result of this is that the shrub-community changes from the rank of a stratum society to that of a definite association.

Two associations, whose dominants always occur in consociations, are distinguished as making up the forest under discussion, together with the *Eucalyptus-Doryphora* ecotone. Their distribution, structure, physiognomy and stratum societies are described. In the comments on the relation of forest fires to these communities it is pointed out that the essential oils of an inflammable nature contained in the leaves do not of themselves make burning possible as the fires travel mainly through the substratum where the percentage of oil-containing types is not high. It is rather the low moisture-content of the leaves that favours the fires.

An interesting discussion is also given on the relation of the dehiscence of fruits to the periodic fires and the effect on the population in the early stages of the resulting subseres.

The latter part of the paper discusses in detail the shrub (stratum) societies of an exposed westerly headland and of the Junction Flora.

The system on which the author is working, as well as the scheme of work determined, is of much interest. It should prove of assistance in indicating to workers on similar problems extending over large areas the means of approach and the development of the first general stages in studies of vegetation.

T. F. C.

CYPERUS ROTUNDUS L. IN INDIA.

Ranade, S. B. and **Burns, W.** "The Eradication of *Cyperus rotundus* L. (a study in pure and applied botany)." *Memoirs of the Department of Agriculture in India.* Botanical Series, **13**, 93 pp. and 8 plates.

The memoir contains a full description of this troublesome weed and of several series of experiments conducted with a view to establishing some standard method for its eradication. The plant has several interesting features. Its rate of seed production is fairly high but germination is erratic. It survives chiefly by the production of underground tuber-forming rhizomes, some of which are positively geotropic and may reach a depth of 2·5 feet.

Extensive experiments were undertaken to determine the viability of the tubers under varying external conditions. The authors consider that the features in the life cycle which lend themselves to attack are the inability of the plant to flourish in a close community, e.g. in a thick growth of Saun hemp, and the fact that the tubers usually fail to survive after a fortnight at 40° C.—the temperature of the upper soil during the hot season.

The description of the work is very full and the experimental data are given in great—perhaps too great—detail. The outlook of the writers on the plant's life is extremely anthropomorphic, thus a deep-seated tuber is described as "concentrating all its powers in making one supreme attempt to get to the surface and not wasting material on several ascending organs."

Economically the work achieves its object, scientifically it opens up a host of semi-physiological problems which bid fair to be of great interest—e.g. the reaction of the external conditions on the plant's physiological processes, causing some rhizomes to be positively geotropic; or again the reason why one bud develops from a deep-seated tuber and several from one which is more superficially situated. It is to be hoped that the authors may find opportunity for the further autecological investigation of the species.

S. M. W.

ARID SOUTH AFRICA.

Cannon, W. A. "General and Physiological Features of the more arid portions of Southern Africa, with Notes on the Climatic Environment." *Carnegie Institution, Washington.* Publ. No. 354, 1924, pp. 1–159. 31 plates and 13 figs. in the text.

This volume is a companion to the author's work on arid South Australia which was reviewed in this *Journal* two years ago (**12**, p. 338, 1924). The arrangement and treatment of the subject matter are very much the same in the two volumes and several of the general remarks that were made in the former review might be applied equally to the present work.

The area in South Africa which has a more or less markedly arid climate and vegetation is large and the present account makes no attempt to give a complete picture of the region. It is a record of the author's observations made at a series of selected places during his visit to South Africa. This method of treatment of a large area by the description of selected samples has certain inherent drawbacks which are apparent in reading this volume. There is a considerable degree of discontinuity and the relationships of communities to the environment and to one another are lost sight of. In any case, however, Dr Cannon centres attention on representative plants and the adjustment of these to environmental conditions rather than on, indeed almost to the exclusion of, plant communities.

In the first part of the book a general account of the climatic and other features of South Africa are given; such features as temperature, rainfall, wind, and humidity of the air are considered. Under rainfall, special attention is paid to the seasonal distribution and to the occurrence and duration of drought periods. An attempt is made also to determine the amount of the total precipitation which is "effective" and "non-effective." Evaporation was also studied; and for this purpose Dr Cannon introduced a number of porous cup

atmometers of the L[illegible] type. This was the first time such instruments had been used in the country[illegible] atmometers were established at a number of representative stations, but in most [illegible] they were not running for a sufficient length of time to allow of any generalisations to be made from the figures published. Also the results, such as they are, are to some extent vitiated by the great variability of the instruments when they were restandardised after use. The account of the climatic factors is followed by a very general description of the main types of vegetation and of the botanical regions but in this portion nothing new is added to the accounts previously published.

The description of the author's own observations follows this general introduction, observations which were made at selected stations, in the Namib in South West Africa, and at three stations in the Central and Western Karroo, Beaufort West, Prince Albert Road, and Majesfontein. General descriptions of the vegetation and topography at each station are given, but unfortunately these are so short that it is exceedingly difficult, if not impossible, for a reader, who is unacquainted with the ground, to make any clear picture.

At the Karroo stations quadrat enumerations of the perennial plants were made which give a good indication of the degree of local variation in the flora of these regions. Thus at Majesfontein four quadrats, each 10 meters square, had respectively: 49 individuals, all sclerophylls; 345 individuals, all sclerophylls; 330 (170 succulents); and 397 (213 succulents).

Some notes are given on the root habits: the succulents as a rule have a meagre root system which is mainly superficial although exceptions were noted in *Euphorbia multiceps* and *Pelargonium crithmifolium*, where the main root descended to deep levels and did not form superficial roots. This phenomenon occurs in many other species of *Euphorbia*. The sclerophylls have generally a much larger development of roots. Some cases of root budding are noted.

The next section deals with the structure of the foliar organs of a considerable number of the plants. The leaf structure showed very great variety, and the influence of the environment seems to have been in the direction of the development of xerophytic features on various plans of structure. A summary of some of the features of the families is given, their distribution considered and suggestions as to the lines along which the structural modifications have occurred are put forward.

The final portion deals with the foliar transpiring power of the plants in winter and spring. The observations were made for the most part in the Karroo and the experiments were made by the Stahl-Livingston cobalt chloride method, a method that has great advantages for such field studies. A variety of plants was investigated, succulents, sclerophylls, and some geophytes. While the results are rather fragmentary and were all made in winter, they do show certain features of interest. The index was found to fall during the day; in the sclerophylls the maximum occurred in the early morning; in the succulents it is at night. The maximum itself is in many cases exceedingly low. It is interesting to note, in passing, that a few tests, made on *Welwitschia*, gave a surprisingly high index, which suggests that, in spite of the habitat, this peculiar plant may not be quite so extreme a xerophyte as it is sometimes thought to be.

The volume as a whole leaves the reader with a feeling of lack of satisfaction, almost of disappointment. This is due mainly to the great discontinuity in the treatment of the subject matter. The book is really a series of field notes and not one whole; many subjects are touched upon but of none of them is there anything like a full account, and the passage from one to the other is abrupt. The resulting impression on the reader is of a series of isolated fragments. But, in spite of these drawbacks, which are to some extent inseparable from the methods of study and treatment, Dr Cannon's book should be of value in drawing the attention of botanists, and especially of South African botanists, to an extremely interesting vegetation which presents a very great number of problems for investigation. His results, all of which are necessarily of a preliminary kind, should act as a stimulus to others to undertake detailed work in these regions. The book is illustrated by a number of excellent photographs.

R. S. A.

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